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THE EFFECT OF BREEDING ON FEEDLOT PERFORMANCE AND CARCASS CHARACTERISTICS OF LAMBS AS DETERMINED BY FEEDING TRIALS AND CARCASS TESTS[1]

A COMPARISON OF RYELAND × RAMBOUILLET, ROMNEY × RAMBOUILLET, CANADIAN CORRIEDALE AND RAMBOUILLET FEEDER LAMBS

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For several years sheep breeding projects have been in progress for the purpose of developing a new and superior breed of sheep for the range lands of Western Canada. In the fall of 1937 it was decided to conduct a feeding trial and carcass study at the Lethbridge Experimental Station to compare the rate and economy of gains and the market suitability of lambs from the different projects.

The four lots included in the trial were, Ryeland × Rambouillet lambs from the University of Saskatchewan, Romney × Rambouillet, grade Rambouillet lambs from Kirkvold Brothers' ranch at Manyberries, and Canadian Corriedale lambs from the ranch of M. L. Holtman of Skiff. The trial was repeated the following year (1938–1939).

MATERIALS AND METHODS

Breeding of the Lambs Used in the Feeding Trials

As the purpose of the experiment was to compare lines of breeding it is in order at this point to review briefly the breeding history of the four groups.

The University of Saskatchewan lambs resulted from crossing imported Ryeland rams on Rambouillet ewes; the Romney cross lambs supplied by Kirkvold Brothers, and raised at the Dominion Range Experiment Station, Manyberries, resulted from crossing Romney rams, obtained in the United States, on Rambouillet ewes; the lambs from the Holtman ranch were the result of successive crosses of Canadian Corriedale rams on Rambouillet ewes and subsequent generations of cross-bred ewes. A few New Zealand Corriedale rams were also used. The lambs of the Corriedale group were second and third cross, while in the other groups first cross lambs were used with the exception that a few F_2 lambs were included in the 1938–39 Romney cross group. It will be noted that in all three lines of breeding the original cross was on Rambouillet ewes and thus a group of grade Rambouillet lambs served as a control group.

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Summer Management and Selection of the Lambs for the Experiment

In an experiment such as this the feed lot results are influenced by the previous management and development of the lambs and also by the degree to which each selected group truly represents the breed group from which it is drawn.

In general the lambs in these experiments had received similar treatment during their growing period. They were born and raised under range conditions, though these conditions were not identical. The Ryeland cross lambs were raised in the sandhills country south of Saskatoon, whereas the other three groups were raised on the short-grass range lands of south-eastern Alberta.

The selection of the lambs was originally planned so that they would represent truly the bands from which they were taken and they were to be of similar average initial weight. Practical limitations, especially shortage of material in the Romney cross group, resulted in some deviation from the original plan. Differences in initial weight are indicated in Tables 1A and 1B.

Wether lambs were used in all groups except that a few ewe lambs were included in the Canadian Corriedale group in the 1937–38 trial.

TABLE 1A.—TABLE OF RESULTS 1937–38 LAMB FEEDING TRIAL

——	Group I Ryeland Cross	Group II Romney Cross	Group III Corriedale	Group IV Rambouillet
Original number of lambs in group	40	40	40	40
Death losses	0	0	0	0
Number of lamb days	3355	4622	4762	4391
	lb.	lb.	lb.	lb.
Initial weight of group	2819.0	2793.0	2510.5	2954.5
Average initial weight of lambs	70.5	69.8	62.8	73.9
Final weight of group	3975.0	4280.0	3981.0	4292.0
Ave. final weight of lambs	99.4	107.0	99.5	107.3
Total gain	1156.0	1487.0	1470.5	1337.5
Average gain	28.9	37.2	36.8	33.4
Average daily gain	.34	.32	.31	.30
Feed Consumed:				
Alfalfa hay	7340	9410	9580	9040
Oats	1558	2213	2192	2147
Barley	2650	3959	3919	3827
Total grain	4208	6172	6111	5974
Salt	75	75	75	75
Ave. Feed Consumption per Lamb:				
Alfalfa hay	183.5	235.2	239.5	226.0
Oats	39.0	55.3	54.8	53.7
Barley	66.2	99.0	98.0	95.7
Total grain	105.2	154.3	152.8	149.4
Salt	1.88	1.88	1.88	1.88
Feed Consumed per Pound of Gain:				
Alfalfa hay	6.3	6.3	6.5	6.8
Oats	1.3	1.5	1.5	1.6
Barley	2.3	2.7	2.7	2.9
Total grain required per pound of gain	3.6	4.2	4.2	4.5

TABLE 1B.—TABLE OF RESULTS 1938–39 LAMB FEEDING TRIAL

——	Group I Ryeland Cross	Group II Romney Cross	Group III Corriedale	Group IV Rambouillet
Original number of lambs in groups	40	40	40	40
Death losses	1 (Nov. 26)	0	1 (Dec. 31)	0
Number of lambs marketed	39	40	39	40
Number of lamb days	3267	4390	4205	4488
	lb.	lb.	lb.	lb.
Initial weight of original lambs	3097.0	2700.0	2644.0	2759.0
Initial weight of lambs which completed the trial	3016.5	2700.0	2588.5	2759.0
Average initial weight of lambs which completed the trial	77.3	67.5	66.4	69.0
Final weight of group*	3768.0	3906.0	3767.0	3959.0
Average final weight of lambs*	96.6	97.6	96.6	99.0
Total gain	751.5	1206.0	1178.5	1200.0
Average gain	19.3	30.2	30.2	30.0
Average daily gain	.23	.27	.28	.27
Feed Consumed†				
Alfalfa hay	8230	10770	10022	10380
Oats	1226	1593	1538	1653
Barley	2857	4005	3841	4185
Total grain	4083	5598	5379	5838
Salt	49	65	65	62
Average Feed Consumption per Lamb:				
Alfalfa hay	211.0	269.2	257.0	259.5
Oats	31.4	39.8	39.4	41.3
Barley	73.2	100.1	98.5	104.6
Total grain	104.7	140.0	137.9	146.0
Salt	1.26	1.62	1.67	1.55
Feed Consumed per Pound of Gain:				
Alfalfa hay	10.9	8.9	8.5	8.6
Oats	1.6	1.3	1.3	1.4
Barley	3.8	3.3	3.2	3.5
Total grain required per pound of gain	5.4	4.6	4.6	4.9

* Final weight taken as net weight at Calgary.
† The feed consumed by the lambs which died was calculated and subtracted from the total feed consumption in each case (Ryeland and Corriedale).

Procedure for the Feeding Trials

Forty lambs were used for each group in both feeding trials. At the commencement of the trials the lambs were branded with numbers, and individually weighed on two successive days. The average of the two weights was taken as the initial weight for each lamb and the initial weight for each pen was arrived at by adding the individual weights. As the trials progressed individual weighings were made at various intervals including the final weight when the lambs were sold.

It was planned that all of the lambs would be disposed of when fat, irrespective of weight, and in the second trial this procedure was closely followed. The only exception in this trial was in the case of the first lot

marketed in which a delay, pending completion of arrangements with Burns and Company for disposal of the lambs, resulted in some of the Ryeland cross lambs being held on feed longer than would normally have been the case. In the first trial, due to the necessity of regulating disposals to suit the limited capacity of the local plant, it was not always possible to dispose of the lambs at the optimum time.

The 1937–38 trial was started October 18 and the 1938–39 trial on October 21. In each case the groups were started on 5 pounds of oats per group with gradual increases and changes in rations being made. The final mixture used in the first trial was 2 barley : 1 oats, and in the second trial 3 barley : 1 oats.

In the first trial the plan was to keep all lambs on the same average amount of grain as long as possible but this was not entirely satisfactory. The second year the rate of feeding was governed by the consuming ability of each group. This procedure prevented the rather serious digestive disturbances experienced the first year when a number of lambs, especially in the Corriedale group, went off feed.

Second cut alfalfa hay of good quality was fed in such amounts as would readily be cleaned up without undue waste. The coarse stems which were left over were not weighed back, but the hay remaining in the bins for each pen was weighed back at the end of each feeding trial and the hay actually fed was recorded. Hay and grain were fed twice daily in combination troughs. Salt was available to the lambs at all times.

Some difficulty was experienced with soremouth in both trials and it was necessary to treat some of the Rambouillet lambs. The condition was not serious but probably did cause a slight setback to the lambs. In the second trial a few lambs in the other groups were affected but were not treated as they were well on the way to recovery by the time they were started on feed.

The results of the feeding trials are presented in the discussion and tables which follow. Some differences between groups were discovered from an analysis of the data, but greater uniformity of conditions during the range period would add more weight to these results.

DISCUSSION OF RESULTS

From Tables 1A and 1B it will be seen that the differences between the Romney cross, Corriedale and Rambouillet groups were very slight and the relative performance was quite similar in the two trials.

The fact that in the second trial net weights at Calgary were used as the final weights and that weights off feed were used in making calculations for the first trial may account for a considerable part of the differences between years with respect to gains per day and feed requirements per pound of gain.

Notwithstanding the differences between years, both with respect to initial weight and marketing procedure as noted above, it is a striking feature that the total grain requirements per pound of gain for the Romney cross, Corriedale, and Rambouillet groups bore the same relationship in the second as in the first feeding trial. Equally striking is the lack of agreement between the results of the Ryeland cross groups in the two trials.

Correlation coefficients were calculated to determine whether or not the initial weight of the lambs had any bearing on their subsequent rate of gain.

TABLE 2.—CORRELATION BETWEEN INITIAL WEIGHT AND RATE OF GAIN

Independent Variate (Initial weight in pounds) = A
Dependent Variate (Rate of gain in pounds per day) = X

Year	Group	No. of pairs	Correlation coefficient	P	Regression coefficient, X, A	Regression equation
1937–38	Ryeland Cross	40	−.069	>0.05		
1938–39	Ryeland Cross	39	−.399	<0.05	−.002,6	$\bar{x} = .4242 - .0026$
1937–38	Romney Cross	40	.114	>0.05		
1938–39	Romney Cross	40	−.117	>0.05		
1937–38	Corriedale	40	.456	<0.01	.005,7	$\bar{x} = -.0422 + .0057$
1938–39	Corriedale	39	−.222	>0.05		
1937–38	Rambouillet	40	.182	>0.05		
1938–39	Rambouillet	40	−.298	>0.05		

Only 2 of the 8 lots showed a significant correlation between initial weight and rate of gain, namely, the 1937–38 Corriedale groups and the 1938–39 Ryeland cross group. The highly significant correlation in the case of the Corriedales was positive, indicating that the lambs which were heaviest at the commencement of the trial made the fastest gains. The positive correlation coefficients for the 1937–38 Romney Cross and Rambouillet groups, although not statistically significant, indicate a similar tendency. These results are in agreement with the observation that some of the smaller lambs in the 1937–38 groups went off feed and that the Corriedale group was most affected in this respect and the Ryeland cross group least affected.

The smaller lambs fed in the second trial did not receive a setback and had a tendency to make more rapid gains than the larger lambs as indicated by the negative correlation coefficients. A statistically significant correlation of −0.399 was found in the case of the Ryeland cross group.

Tables 3A and 3B show the rate of gain made by the lambs for 28-day periods and also, in the 1937–38 trial, for 14-day periods. For each period, only those lambs on feed for the entire period are included.

It will be noted that in the first trial the Ryeland cross group made the fastest gains up to the period December 28 to January 11. By the time they did fall off in rate of gain only 18 lambs remained. In the second trial the Ryeland cross group made the fastest gains in the December 17 to January 14 period, but in the January 14 to February 11 period, in which lambs of the other groups made still faster gains, no Ryeland cross lambs remained. Thus the decline in rate of gain which occurred in all groups in the first trial and the increase in rate of gain in all groups towards the latter part of the second trial affected some groups more than others.

It will be noted that in the first feeding trial the variations in rate of gain were greater than in the second trial. In general these variations

agreed rather closely with observed conditions. The lowered rate of gain in the Rambouillet group in the November 16 to 30 period corresponds with the time at which soremouth appeared in that group. Also the lowered rate of gain of the Corriedale group (November 30 to December 14) corresponds with the period in which the lambs of that group first went off feed. Later the grain consumption of all the lambs declined with a corresponding decrease in rate of gain.

TABLE 3A.—AVERAGE GAINS AND AVERAGE GAINS PER DAY MADE BY LAMBS ON FEED 1937–38

Group	Oct. 19 – Nov. 16 (28 days)			Nov. 16 – 30 (14 days)			Nov. 30 – Dec. 14 (14 days)		
	No.	Ave. gain	Ave. gain per day	No.	Ave. gain	Ave. gain per day	No.	Ave. gain	Ave. gain per day
		lb.	lb.		lb.	lb.		lb.	lb.
I Ryeland Cross	40	8.9	.32	40	4.7	.34	30	6.8	.48
II Romney Cross	40	8.0	.28	40	5.4	.39	39	4.7	.33
III Corriedale	40	9.3	.33	40	5.1	.37	38	3.7	.26
IV Rambouillet	40	7.2	.26	40	3.3	.24	40	6.4	.46
	Dec. 14 – 28 (14 days)			Dec. 28 – Jan. 11 (14 days)			Jan. 11 – Feb. 8 (28 days)		
I Ryeland Cross	30	5.6	.40	18	1.1	.08	—	—	—
II Romney Cross	39	4.4	.32	38	4.0	.28	26	8.2	.29
III Corriedale	38	3.8	.27	38	1.7	.12	27	9.8	.35
IV Rambouillet	40	4.7	.33	36	2.5	.18	21	9.0	.32

TABLE 3B.—AVERAGE GAINS AND AVERAGE GAINS PER DAY MADE BY LAMBS ON FEED 1938–39

Group	Oct. 21 – Nov. 21 (30 days)			Nov. 21 – Dec. 17 (26 days)			Dec. 17 – Jan. 14 (28 days)			Jan. 14 – Feb. 11 (28 days)		
	No.	Ave. gain	Ave. gain per day	No.	Ave. gain	Ave. gain per day	No.	Ave. gain	Ave. gain per day	No.	Ave. gain	Ave. gain per day
		lb.	lb.		lb.	lb.		lb.	lb.		lb.	lb.
I Ryeland Cross	39	7.6	.25	39	7.2	.28	29	9.4	.34	—	—	—
II Romney Cross	40	7.5	.25	40	7.4	.29	38	7.9	.28	24	12.3	.44
III Corriedale	39	8.7	.29	39	6.6	.25	39	7.5	.27	23	13.6	.48
IV Rambouillet	40	7.6	.25	40	7.5	.29	36	7.0	.25	29	11.2	40

In the second trial, aside from scouring in a few of the Ryeland cross lambs, and some soremouth in the Rambouillets, no conditions were noted which might be expected to affect the gains.

CONCLUSION

On the basis of the two trials it appears that the differences between the four groups are relatively slight, and more refined methods and greater control during the pre-feeding growth period are essential if hereditary differences are to be measured.

SUMMARY

(1) Two feeding trials were conducted to compare the rate and economy of gains of Ryeland × Rambouillet, Romney × Rambouillet, Corriedale, and Rambouillet feeder lambs.

(2) The Romney cross, Corriedale and Rambouillet groups did not differ greatly in rate of gain in either trial with gains of 0.32, 0.31, and 0.30 pound per day respectively in the first trial and 0.27, 0.28, and 0.27 pound per day in the second trial.

(3) The three groups ranked in the same order in both trials with respect to amount of grain required to produce a pound of gain. The Romney cross lambs required 4.2 pounds of grain in the first trial and 4.6 pounds in the second, the Corriedales 4.2 pounds and 4.6 pounds, and the Rambouillet 4.5 pounds and 4.9 pounds.

(4) The Ryeland cross lambs made the fastest gains in the first trial (0.34 pound per day) and the slowest gains in the second trial (0.23 pound per day). In the first trial it required 3.6 pounds of grain to make a pound of gain and in the second trial 5.4 pounds of grain were required.

(5) Correlation coefficients were calculated to determine whether the initial weight of the lambs had any bearing on the subsequent rate of gain. A significant positive correlation was found in the case of the 1937–38 Corriedale group and a significant negative correlation in the case of the 1938–39 Ryeland cross group.

(6) There were extreme variations in rates of gain within groups. In come cases variations in rate of gain agreed closely with observed conditions, i.e., the appearance of soremouth in the Rambouillet group in both trials and the fact that some lambs, particularly the Corriedales, went off feed in the first trial.

SLAUGHTER AND CARCASS TESTS, 1938-39

Limited data on carcass measurements and cuts were obtained in the 1937–38 experiment. These were presented in an earlier unpublished report and as they constituted preliminary data obtained in developing procedure they will not be included in the present report. They will be referred to from time to time to bring out differences and similarities in the results from the two experiments. Only the analyses of data obtained in the 1938–39 experiment will be presented in this report.

Procedure in Handling Lambs for the Slaughter Test

Lambs for slaughter were selected by handling each lamb that appeared finished. The selected lambs were trucked to Burns & Co., Calgary, and were killed at the abattoir of that company. Routine slaughter procedure was followed, with the experimental lambs following the regular day's kill. Individual identification was maintained throughout.

The carcasses were permitted to cool overnight and, after official grading, representative carcasses were cut and the weights and measurements taken.

RESULTS

The Slaughter Test

Referring back to Table 1B, page 155, it will be seen that, although the average initial weights and average gains of the groups differed greatly,

the average final weights were very similar, with the Ryeland cross and Corriedale groups being lightest at 96.6 pounds and the Rambouillets heaviest at 99.0 pounds. It is also worthy of note (Table 1A) that although the average final weights in the first trial showed greater differences between groups than those of the second trial, the same relationship existed between breed groups, with the Ryeland cross and Corriedale lambs finishing at a lighter weight than the lambs of the other two groups.

From the data of the second trial an analysis of variance of initial weights, final weights and gains was made and appears in Table 4. It will be noted that the differences between groups in initial weights and gains were statistically significant though they were fairly consistent for the two years.

TABLE 4.—ANALYSIS OF VARIANCE IN INITIAL WEIGHTS, FINAL WEIGHTS, AND GAINS OF LAMBS FED IN 1938–39 FEEDING TRIAL

Measurement	Source of variation	*D/f*	Sums of squares	Mean square	*F*[x]
Initial weight lb.	Total	157	11,598.00		
	Between lots	3	2,910.00	970.00	
	Within lots	154	8,688.00	56.42	
					17.19 H.S.
Final weight lb.	Total	157	6,579.35		
	Between lots	3	150.45	50.15	
	Within lots	154	6,728.90	43.69	
					1.15 N.S.
Gain lb.	Total	157	11,299.49		
	Between lots	3	3,460.57	1,153.52	
	Within lots	154	7,838.92	50.90	
					22.66 H.S.

[x] N.S.—Not significant. S.—Significant. H.S.—Highly significant.

An analysis of variance of warm carcass weights of all carcasses and of the carcasses which were cut is shown in Table 5.

TABLE 5.—ANALYSIS OF VARIANCE IN WARM CARCASS WEIGHTS OF ALL CARCASSES AND OF CARCASSES USED IN THE CARCASS TEST, 1938–39

	Source of variation	*D/f*	Sums of squares	Mean square	*F*
All carcasses	Total	157	2,211.00		
	Between lots	3	20.59	6.86	
	Within lots	154	2,190.41	14.22	
					— N.S.
Carcasses cut	Total	74	1,171.00		
	Between lots	3	69.54	23.18	
	Within lots	71	1,101.46	15.51	
					1.49 N.S.

This analysis permits the assumption that the carcasses selected for cutting were representative of their respective groups.

The average carcass weights are shown in Table 6.

TABLE 6.—AVERAGE CARCASS WEIGHTS OF ALL CARCASSES AND CARCASSES CUT

	Ryeland Cross		Romney Cross		Corriedale		Rambouillet	
	No.	Ave. wt.	No.	Ave. wt.	No.	Ave. wt.	No.	Ave. wt.
		lb.		lb.		lb.		lb.
All carcasses	39	47.44	40	47.98	39	48.41	40	48.20
Carcasses cut	16	46.40	20	49.15	19	47.21	20	47.75
Deviations		−0.94		+1.17		−1.20		−0.45

TABLE 7.—AVERAGE DRESSING PERCENTAGES FOR THE FOUR GROUPS, 1937–38 AND 1938–39

	Ryeland Cross		Romney Cross		Corriedale		Rambouillet	
	No.	%	No.	%	No.	%	No.	%
1937–38	29	50.4	18	49.6	21	49.9	16	49.5
1938–39	39	49.1	40	49.1	39	50.1	40	48.7

TABLE 8.—WEIGHTS OF CUTS FROM CARCASSES CUT IN 1938–39 CARCASS TEST

			Ryeland × Rambouillet	Romney × Rambouillet	Corriedale	Rambouillet	Necessary difference (N = 16)
	Number of lambs		16	20	19	20	
	Average weight of carcasses	lb.	46.5	49.2	47.2	47.8	
Leg	Total weight	lb.	213.1	285.1	254.0	275.8	
	Average weight	lb.	13.3	14.3	13.4	13.8	
	Percentage of total carcass weight	%	29.0	29.3	28.6	29.0	
Middle	Total weight	lb.	220.6	295.2	279.9	295.9	
	Average weight	lb.	13.8	14.8	14.7	14.8	
	Percentage of total carcass weight	%	30.1	30.3	31.5	31.1	
Shoulder	Total weight	lb.	156.2	215.9	196.6	206.5	
	Average weight	lb.	9.8	10.8	10.4	10.3	
	Percentage of total carcass weight	%	21.3	22.2	22.1	21.7	
Stew	Total weight	lb.	144.0	178.0	157.6	172.5	
	Average weight	lb.	9.0	8.9	8.3	8.6	
	Percentage of total carcass weight	%	19.6	18.3	17.8	18.2	.9529

Dressing Percentages

As no significant differences were found in either final live weights or warm carcass weights it would seem probable that no significant difference would be present in the dressing percentages. A statistical analysis was not made but the average dressing percentages for the various groups in both trials are shown in Table 7.

It will be noted that although the differences between groups were small the Rambouillets had the lowest average dressing percentage in both trials.

The Carcass Test

The original plan was to cut as many carcasses as possible but with an equal number from each group. Certain practical difficulties intervened so that only 16 Ryeland cross, 19 Corriedale, and 20 each of the Romney cross and Rambouillet carcasses were cut.

Weights of Carcass Cuts

The data obtained from weights of carcass cuts appear in Table 8.

The cuts designated as "stew" included neck, fore shank, brisket, and fore, and hind leg bones. The brisket cut included the flank. The front cut was made between the fourth and fifth rib and the leg cut was made in front of the hip bone and at right angles to the cutting block. This latter cut was not very accurately defined but it was observed that the point of cutting did not vary to any appreciable degree.

TABLE 9.—ANALYSIS OF VARIANCE IN PER CENT OF CARCASS WEIGHT IN THE VARIOUS CUTS. 1938–39 CARCASS TEST

Measurement	Source of variation	*D/f*	Sums of squares	Mean square	*F*
Weight of Leg as percentage of total carcass	Total	74	127.7744		
	Between lots	3	4.5960	1.5320	
	Within lots	71	123.1784	1.7349	— N.S.
Weight of Middle as percentage of total carcass	Total	74	328.4159		
	Between lots	3	27.6241	9.2080	
	Within lots	71	300.7918	4.2365	2.17 N.S.
Weight of Shoulder as percentage of total carcass	Total	74	132.5753		
	Between lots	3	7.6040	2.5347	
	Within lots	71	124.9713	1.7601	1.44 N.S.
Weight of Stew as percentage of total carcass	Total	74	147.3613		
	Between lots	3	33.7140	11.2380	
	Within lots	71	113.6473	1.6007	7.02 H.S.

Each carcass cut was calculated as a percentage of the total carcass weight and an analysis of variance was calculated from these data (Table 9). The differences between breeds were small and only in the case of the stew was there a difference sufficiently great to be statistically significant.

A necessary difference was calculated from the mean square according to the procedure of Crampton and Hopkins (1934). It will be observed that on the average the Ryeland cross lambs were significantly higher in percentage of stew than any of the other groups. There were no significant differences between the Romney cross, Corriedale and Rambouillet groups.

The higher percentage of carcass weight represented by stew in the Ryeland cross group is believed to have been due to heavier briskets. The briskets were not weighed separately but they represented the largest single item in the stew cut and it was observed that the Ryeland cross lambs were deeper and broader in the brisket than the other lambs.

Measurement of Carcasses

Measurements were made according to a standard procedure and the data are summarized in Table 10.

TABLE 10—MEASUREMENTS OF CUTS FROM CARCASSES CUT IN 1938–39 CARCASS TEST (INCHES AND 10THS)

		Ryeland × Rambouillet	Romney × Rambouillet	Corriedale	Rambouillet	Necessary difference N = 16
Spring of rib	Number	16	20	20	20	
	Total	117.2	145.7	146.9	141 9	
	Average	7.32	7.28	7.34	7.10	
Length of middle	Number	16	20	20	20	
	Total	267.3	338.8	339.4	348.2	
	Average	16.71	16.94	16.97	17.41	
Fat	Number	16	20	20	20	
	Total	5.10	5.05	6.25	4.25	
	Average	.32	.25	.31	.21	.0920
Leg (H. to H.)	Number	16	20	20	20	
	Total	163.9	211.2	210.0	216.1	
	Average	10.24	10.56	10.50	10.80	
						.3380
Leg (circumference)	Number	16	20	20	20	
	Total	97.5	129.9	123.0	124.0	
	Average	6.09	6.50	6.15	6.20	
Loin muscle (length)	Number	16	20	20	20	
	Total	34.8	43.1	43.1	44.3	
	Average	2.18	2.16	2.16	2.22	
Loin muscle (width)	Number	16	20	20	20	
	Total	19 3	23.6	23 3	23 5	
	Average	1.21	1.18	1.16	1.18	

It is doubtful if adequate measurements of the more important carcass characteristics, namely, fullness of leg and muscling at the loin, were obtained. For example, measurements of maximum length and width of loin muscle only tell part of the story as the measurements do not take into account the shape of the loin muscle. An oval shaped loin muscle would include a larger amount of meat than a diamond shaped one and for this reason a planimeter would be more satisfactory for making loin muscle measurements. The measurement of leg circumference, taken at a point one-third of the distance from hock to aitch bone, obviously does not give a fair measure of fullness of leg.

The analysis of the data on carcass measurements is shown in Table 11.

Of the seven sets of measurements taken, only two showed statistically significant differences between groups, those being thickness of fat over the loin and length of leg, measured from aitch bone to hock.

The necessary differences between groups in fat thickness and length of leg were calculated from the mean squares and are included in Table 10. By comparing the four groups in all possible combinations with respect to each of the two items it will be observed that: *(a)* the average thickness of

TABLE 11.—ANALYSIS OF VARIANCE IN MEASUREMENTS OF CUTS FROM CARCASSES CUT IN 1938–39 CARCASS TEST

Measurement	Source of variation	*D/f*	Sums of squares	Mean square	*F*
Spring of rib	Total	75	8.34		
	Between lots	3	.76	.2533	
	Within lots	72	7.58	.1053	2.40 N.S.
Length of middle	Total	75	51.67		
	Between lots	3	4.79	1.60	
	Within lots	72	46.88	.6511	2.46 N.S.
Fat	Total	75	1.2167		
	Between lots	3	.1461	.0487	
	Within lots	72	1.0706	.0147	3.27 S.
Leg (H. to H.)	Total	75	17.35		
	Between lots	3	2.85	.9500	
	Within lots	72	14.50	.2014	4.72 H.S.
Leg (circumference)	Total	75	20.05		
	Between lots	3	1.84	.6133	
	Within lots	72	18.21	.2529	2.42 N.S.
Loin muscle (length)	Total	75	1.36		
	Between lots	3	.04	.0133	
	Within lots	72	1.32	.1833	— N.S.
Loin muscle (width)	Total	75	1.26		
	Between lots	3	.01	.003	
	Within lots	72	1.25	.017	— N.S

fat in the Rambouillet group was significantly less than the corresponding measurement in the Ryeland cross and Corriedale groups; *(b)* the average length of leg in the Rambouillet group was significantly greater than that of the Ryeland cross group; and *(c)* there were no other significant differences between groups.

The average of the fat measurements for the Ryeland cross and Corriedale groups of 0.32 and 0 31 inch respectively, compared to measurements for the Romney cross and Rambouillet groups of 0.25 and 0.21 inch respectively, agree with the observation that the former two groups not only finished at lower weights than the others but reached a higher degree of finish. It is worthy of note in this connection that, although the Corriedales and Romney cross lambs made practically identical performances in respect to rate of gain and utilization of feed, they did differ in degree of finish at the time of disposal.

Wastiness, or a high proportion of fat to lean, is an undesirable feature from the standpoint of economy but a comparison of groups in this respect could not be made on a basis of the above measurements. Then too it would be impossible to state to what extent the wastiness which was encountered was the result of breed and to what extent the result of some

lambs being held too long on feed. As noted previously, the first lot of Ryeland cross lambs to be marketed did include some lambs which were overfinished.

The leg measurement from aitch bone to hock, which is virtually a measure of "legginess", showed that when all of the groups were considered, the Ryeland cross lambs had the shortest legs on the average and the Rambouillets the longest. It is interesting to note that, although a different measurement for "legginess" was used in the 1937–38 carcass test, namely, length of shank, the same general conclusions were reached as illustrated below.

	Ryeland Cross	Romney Cross	Corriedale	Rambouillet Cross
1937–38 Ave. length of shank = Inches	8.0	8.0	8.0	8.6
1938–39 Ave. length of leg = Inches	10.2	10.6	10.5	10.8

Although the above figures are for different measurements taken on different lambs it appears that the legginess observed in the Rambouillet lambs is to be accounted for both by length of shank and length of leg above the hock.

General Comments on The Carcasses

During the course of the slaughter and carcass test, notes were made from time to time, including observations made by Burns & Company employees and others who had occasion to inspect the carcasses. Some of the notes are believed to be of sufficient interest to be included in this report.

(1) *Grading of the Lambs.* All of the lambs were graded as number one except three which graded Number two, and included: one Ryeland cross, one Romney cross, and one Rambouillet. With such a small number failing to reach the top grade out of 158 carcasses, it is obvious that no comparison of groups could be made on the basis of carcass grades.

(2) *Placing of Forty Carcasses on The Rail.* The 40 carcasses from the lambs delivered on January 17 were placed on the rail in order of suitability from the butchers' standpoint, the placings being made by a Burns' Company employee. The final placing simply illustrated the great variation within groups. Unfortunately the lot contained only one Rambouillet along with seven Romney cross, nine Corriedales, and twenty-three Ryeland cross lambs. Although Ryeland cross lambs were placed first and third they also held the bottom three places. Similarly the Romney cross and Corriedale carcasses ranged from near the top to near the other extreme while the single Rambouillet carcass was placed fourth from the bottom. As conformation, weight, colour of fat, and several other characteristics were used in making the final placings it became apparent that such a comparison of carcasses was not satisfactory. For future work it is suggested that a carcass score card be employed to evaluate qualitative characteristics.

(3) A few carcasses were off colour and at least two (1 Rambouillet and 1 Corriedale) had soft fat.

CONCLUSION

From the results obtained it appears that desirable type market lambs can be produced within all four lines of breeding although the Rambouillets, and to a lesser extent the Romney cross lambs, do not finish as readily as lambs of the other two groups.

SUMMARY—SLAUGHTER AND CARCASS TEST

(1) The 158 lambs which completed the 1938–39 feeding trial were killed at the Burns & Company plant at Calgary where warm carcass weights were obtained: 75 carcasses were cut, and the cuts were weighed and measured according to a standard procedure.

(2) There were no statistically significant differences between groups in final weights or warm carcass weights, indicating that on the average the lambs of the different groups finished at practically the same weight even though they started the trial at considerably different average weights, and were not selected for slaughter on the basis of weight.

(3) The differences between groups in average dressing percentage were not significant although the Rambouillets had the lowest average dressing percentage both in 1937–38 and 1938–39.

(4) There was a statistically significant difference between groups in weight of stew as a percentage of total carcass weight but in the other cuts no significant differences were found. The Ryeland cross group averaged heavier in weight of stew and lighter in weight of shoulder than the other groups, and the Corriedales had the lightest average weight of stew.

(5) The Rambouillet and Romney groups differed from the other two groups in having less thickness of fat over the loin, and this difference was found to be statistically significant in the case of the Rambouillet group. The Rambouillets were more leggy than the other groups and the Ryeland cross lambs had the shortest leg on the average. By statistical analysis the greater length of leg of the Rambouillets was found to be highly significant.

(6) The carcass measurements were not adequate in all cases and revision of the procedure is suggested.

(7) A few notes made during the progress of the trial are included in the report.

ACKNOWLEDGMENT

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REFERENCES

Anonymous. Experimental Slaughter Test for Sheep. Production Service, Dom. Dept. of Agric., Ottawa, Canada. 1938.

Crampton, E. W., and J. W. Hopkins. Analysis of Feeding Trial Data. Jour. of Nutrition, 8 : 338. 1934.

OBSERVATIONS ON MORPHOLOGICAL CHARACTERS AND FLOWERING PROCESSES IN THE SUNFLOWER (*HELIANTHUS ANNUUS* L.)[1]

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INTRODUCTION

A prerequisite to the breeding of sunflowers, as in other crops, is the knowledge of reproductive processes and morphological characters. The development during flowering, the method of pollination, and the time at which fertilization occurs are matters of importance in working out a suitable inbreeding and crossing technique. An estimation of the amount of natural crossing is also of value in determining the breeding methods applicable to the crop. An intimate knowledge of the range of variability of morphological characters is essential as a basis for breeding, and information on the mode of inheritance of such characters is also of value.

When the sunflower breeding work was commenced in 1937 much of this essential information did not appear available in any detailed form. Therefore rather numerous observations were undertaken to secure data concerning the various factors mentioned above. In this paper the results of these investigations for the past three seasons are presented.

LITERATURE REVIEW

Various workers have reported breeding work with sunflowers. Most of this work has been done in Europe, particularly in Russia and Germany. A few references of Canadian and American origin are also available.

Arnoldova (1) reported observations on the flowering behaviour of sunflowers at the Saratov Plant Breeding Station in Russia. Under the conditions prevailing there the stamens of the individual flowers are fully emerged by 5.00 a.m. The dehiscence of the pollen sacs then follows, the pollen collecting on "the upper end of the filament of the stamens", where it remains for 1 to 2 hours, after which it returns into the anthers. About 2.30 p.m. the stigma emerges with closed lobes and at from 3.30 to 7.30 begins to open its lobes. At 7.00 to 8.00 a.m. on the following day it begins to wither and recede, as do the stamens.

The flowering of the whole inflorescence takes 9 to 10 days. On the fourth day the pericarp in the first zone of flowering is darkening. This is explained by the "formation of the 'Panzerchicht', a layer of tissue lying between the sclerenchymatous and cork layers of the tissue of the pericarp". On the twelfth and thirteenth days after flowering commences stripes begin to appear in the seed coat.

Cardon (2) working in Montana reported observations of one year's work on the range of plant type in plots of the Mammoth Russian variety. He noticed variations in such characters as extent of branching, height, strength of main stem, leafiness, seed colour, and time required for maturity.

[1] Contribution from the Division of Forage Crops, Experimental Farms Service, Dominion Department of Agriculture, Ottawa, Canada. Summary of a thesis submitted to the Graduate School of the University of Saskatchewan, in partial fulfilment of the requirements for the degree of Master of Science.

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Hamilton (5) also noticed variation in plant type. He illustrates a number of uniform types, differing in stem character and amount of leaf, which he isolated by inbreeding.

Ross (6), in a study of morphological characters in relation to seed yield and oil content, found highly significant positive correlations to exist between percentage oil and height of plant, percentage oil and yield of seed, and yield of seed and height of plant. Highly significant negative correlations were found between yield of seed and the number of leaves, number of branches, number of heads and number of days from seeding to blooming.

Schiebe (7), discussing the breeding problems of the sunflower in Germany, concludes that the necessary objectives are early maturity, single stemmed type, uniformity, small seed size, high kernel content, and high oil content. Little information is given on the actual breeding methods for securing these objectives.

In a discussion of the specific and varietal characters of sunflowers Cockerell (4) describes 9 species. A type of interest is *Helianthus annuus* var. *chrysanthemoides* in which the heads are entirely double, that is, the corollas of the disc flowers are entirely ligulate. In other work Cockerell (3) describes various colours he found in the ray flowers, and reports the genetic behaviour of some of these colours.

MATERIALS

The foundation material for the investigations reported herein consisted of 500 single head collections made from the fields of 3 Mennonite farmers in the district of Rosthern, Saskatchewan, in September, 1936. In the 1937 season progenies of almost 200 plants of this collection were sown in spaced planted rows. Selections from this group have comprised the major portion of the material used in succeeding years. A few inbred lines were introduced from the Division of Forage Plants, Ottawa, in 1937 and 1938, and a number of introductions of European origin were received from Ottawa in 1939. In addition, 9 introductions were secured from the plant breeding station at Saratov, Russia, in 1937, and 1 possessing varying degrees of red flower colour from Dr. Seager Wheeler at Rosthern in 1938.

All work reported herein is based on observations made with plants grown singly in rows 3 feet apart and spaced every 3 feet within the row, except in the case of material grown for genetic studies in 1939, where the spacing within the row was reduced to 2 feet.

OBSERVATIONS ON MORPHOLOGICAL CHARACTERS

Stem Branching

On the basis of stem character the plants can be divided into two broad general categories: those which produce a single stem and those showing a branching stem with several lateral heads, usually smaller in size than the main central head. The extent of branching and the point or points of origin of the branches varies widely.

One common branching type shows branches from the axils of all the leaves on the main stem with the exception of 2 or 3 leaves near the top

of the stem. In one Ottawa inbred line small secondary branches are found on the main branches. In these cases the more mature secondary heads are carried nearest to the main head.

A further common type among the Mennonite material consists of a basal branching, in which the branches arise from the axils of the leaves at the base of the plant. A great deal of variation in the number and size of the branches in this type occurs. The number may vary from 2 to 8 or 10, and the size from just a few inches in length with no head of importance to a branch over 2 feet in length and bearing a head 2 or more inches across.

As Ross (6) has shown an inverse relationship between the yield of seed and number of branches, it would seem desirable to select toward the single stem type of plant. General observations at Saskatoon support this viewpoint. In addition, the single stem type of plant is more determinate in ripening and yields seed more uniform in size than the branching type of plant.

Stem Strength

Stem strength is a second character showing important variations from the agronomic standpoint. Some inbred lines have a weak stem with a thin long neck which bends over into an inverted U shape, often carrying the head only a few inches from the ground, or, in extreme cases, on the ground. Others show a very stiff erect stem with the seed face forming an angle with the ground surface of 90° or more.

Long leaf petiole and long internodes appear to be associated with the weak stem, and the opposite leaf petiole and internode characters with strong stem.

Seed Coat Colour

The variability of seed coat colour is a matter of common observation. The present investigation shows that the colour depends upon the combination of pigmentation of 3 different seed coat layers. Each of the layers apparently inherits its colour independently of the other two. The condition of the pigment in the various coats can best be detected by examining a seed which is mature but still contains some moisture. At this stage the outer coat, which is membranous, can be peeled off and the second pulpy one scraped away, exposing the third layer, and thus permitting an examination of each region separately.

The outer membranous layer may be clear, or may take a black pigment in stripes, the black stripes varying in width from just a thin line to a condition where almost the entire coat is pigmented. A fully pigmented condition has also been found, but it appears unusual and is probably not comparable to the striped pigment. So far it has been found in only 1 line.

The second layer is corky and may be white or coloured. If coloured, it takes on a solid purple pigment uniformly distributed. Usually this purple pigment is so heavy that it entirely masks the colour of the other coats, and the mature seed appears purple. In the collection of material from Dr. Seager Wheeler, many plants occurred with seed which contained a smaller amount of purple than usual. In this material as the seed dried at maturity the purple turned to brown. Whether this colour is merely

a function of the smaller amount of purple pigment or is due to some chemical agent acting on the purple pigment and changing it to brown is yet undetermined.

The third coloured region is the outermost layer of the rigid part of the seed coat. It probably corresponds to what Arnoldova (1) calls the "Panzerchicht" layer, judging by the position he describes for it, and the fact that it darkens in colour on the fourth day after flowering. In observations at Saskatoon the darkening occurs about 6 days after flowering but several days before the striping appears, which is in general agreement with Arnoldova's finding. The layer takes either a dark brownish black pigment evenly distributed over the whole area of the seed coat or is entirely free of pigment. When coloured it shows through the other areas of the seed coat which are not pigmented as a gray tint. If purple is present in the second coat, the condition existing in the third layer can only be detected by scraping away the second coat.

FIGURE 1. Dissected seeds showing three different layers taking pigment.

Figure 1 illustrates the effect upon the external appearance of the seed of some of the various combinations of colour in the 3 layers. The left column (vertical) shows the normal appearance of 3 different seeds. The centre column shows the outer membranous coat which has been peeled off. In the right column is the remaining portion of the seed, but in each case the right half of the second pulpy layer has been scraped away.

In the lowermost seed it is evident that the only pigmented layer is the outer membranous one which shows a characteristic striping. In the

portion of the seed at the right the 2 colourless layers can be seen. In the centre seed the outer membranous layer is striped and the innermost region is pigmented. The gray colour, due to the pigmented third layer showing through the unpigmented sections of the other two, is observable in the unmutilated portion of the seed. The dark colouring taken by the innermost layer shows clearly in the portion at the right where the second white coat has been removed. The top seed illustrates a case of purple pigment in the second coat. In the undisturbed part the colour appears uniformly dark but the striping in the outer coat is evident when it is peeled off, while the non-pigmented condition of the innermost layer is apparent in the right portion where the second coat has been scraped away.

OBSERVATIONS ON FLOWERING PROCESSES

The Flowering Head

The head of the sunflower is a compound inflorescence composed of many individual flowers in a large disc subtended by large ligulate ray flowers usually yellow in colour. Flowering of the individual flowers normally commences with the opening of the ray flowers, and proceeds from the periphery to the centre at the rate of 1 to 4 rows per day. It should be noted, however, that the arrangement of the flowers on the head is not in concentric circles as the foregoing statement may imply, but in arcs radiating from the centre of the head.

Data collected in 1937 and 1938 on the flowering in a number of heads are presented in Table 1. These data show that about 1 week is required for completion of flowering. The ray flowers fall about 1 day later, and striping in the seed coat begins to appear about 10 days after the commencement of flowering. The data also show that the duration of the processes is not greatly affected by weather, there being little difference in the 2 years. In 1937 precipitation was extremely low, while 1938, though below average, was a year of more normal rainfall.

Two facts not shown by this table warrant mention. First a few scattered flowers around the edge of the disc frequently open and are fertilized before the ray flowers are completely open. Second, often the disc flowers, opening on the same day as the rays, do not form a complete ring around the head, but tend to be confined to one side of it.

TABLE 1.—DURATION OF FLOWERING PROCESSES

Year	No. of plants	Number of days from opening of ray flowers to: Completion of flowering in disc			Appearance of colour in inner seed layer			Appearance of striping			Fall of ray flowers		
		Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.
1937	51	9	5	7	–	–	–	14	4	9.7	12	5	8.4
1938	25	9	6	8	7	6	6.2*	12	9	9.9	11	7	8.2

*4 plants only.

The Individual Flower

Early in the morning on which a given flower on the head opens, its anther tube, formed of 5 united anthers, is exerted by a rapid elongation of the staminal filaments. The filaments reach their full extension about 7.00 a.m. on a normal sunny day. This condition is shown in Figure 2 at the extreme left. Immediately after this stage is reached the pollen sacs discharge their pollen inside the anther tube, as shown in the central three flowers of Figure 2. These flowers have part of the anther tube and the corolla removed to show the pollen sacs. They were dehiscing while the material was being prepared for photographing. This stage is followed by an elongation of the lower portion of the style which pushes the two-lobed stigma up through the anther tube. At the same time there is a loss in turgidity of the staminal filaments and a recession of the anther tube. These two processes result in the pollen being caught on the spiny stigma and pushed out of the upper end of the anther tube. About 5.00 p.m. the tips of the stigma lobes begin to appear, though there is considerable variation depending on the weather conditions and the individual plants. By the following morning the stigma lobes are fully emerged and the receptive surfaces exposed for pollination. In Figure 3 is shown a stage about 8.00 a.m. on the morning of the opening of the flower. The pollen which has dehisced is beginning to appear at the upper end of the anther tube. The condition on the following morning is shown in the flower next to it. The fully emerged, divided stigma lobes and the partly receded anther tube are noticeable. Following exposure of the stigmatic surfaces, pollination and fertilization soon occur, after which the stigma rapidly withers and recedes. On the morning of the second day after the flower opens the processes are completed and the anther and stigma are lying back in the corolla, as shown in the flower on the extreme right in Figure 3.

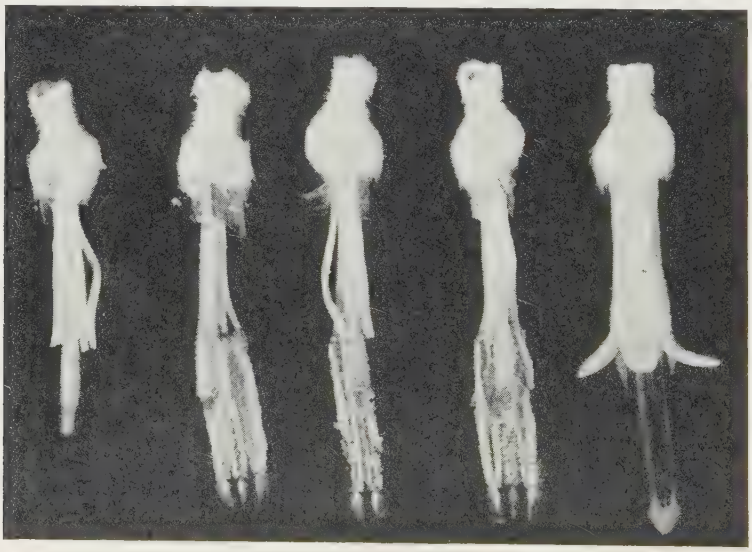

FIGURE 2. Left, a flower showing full extension of anther tube but pollen not dehisced, about 7.00 a.m.; centre, 3 flowers showing dehiscing pollen sacs; extreme right, stigma alone.

FIGURE 3. Development of a flower. Left to right: day prior to opening; day of opening, 8.00 a.m.; day following opening, 8.00 a.m.; fertilized flower, second day after opening.

Stage at which pollen germination commences

To obtain information concerning the stage at which pollen germination commences and to be certain that the inner surfaces of the closed stigma lobes were the receptive surfaces, a number of stigmas were examined at various stages. The times of collection were 7.00 p.m. on the same day that the flowers opened, and 8.00 a.m. and 2.00 p.m. on the day following the opening of the flowers. The collections were made from the same plants on 2 successive days. The first was warm and sunny, and the second relatively cool and cloudy.

Out of a total of 216 stigmas examined in this study none showed germinating pollen grains in a location other than the inner surfaces of the stigma lobes, proving conclusively that these are the receptive surfaces.

The numerical data collected indicate that in most cases sufficient pollen has germinated by 8.00 a.m. on the morning following the opening of a flower to ensure fertilization. It was noticeable that some germination commences immediately the receptive surfaces of the stigma are exposed. Occasional germinated grains were found in collections made at 7.00 p.m. when the stigma lobes were often not even fully emerged from the anther tube. There was also a large variation in the number of germinated grains on different plants at the same time of collection, indicating a predisposition in some plants for germination to proceed faster than in others.

A larger average number of germinated grains was found on the first day at all 3 times of collection, and in most cases the individual plants showed a larger number. This indicates that a more rapid development occurs on a warm, bright day, as compared with a cooler, somewhat overcast day. The difference may be due in part to a slower rate of pollen

germination on the cooler day. However, a more advanced stage of development in the flowering processes was quite noticeable at all 3 times of collection on the first day, which would account to a large degree for the greater number of germinated grains observed.

Pollen tube penetration of the style

To secure an estimate of the stage at which the pollen tube has penetrated through the style and into the ovary a number of plants were treated by removing the stigmas and styles from the flowers at various stages of development. When the heads were mature the seed setting of these plants was compared with plants of the same strain which were not treated. Two plants were treated at each of 5 different stages.

A brief summary of the results from this study is presented in Table 2, showing the percentage seed setting of the treated plants and the corresponding check in each case. Pairs 1 to 4 show that almost no fertilization occurred in the treated plants. In pairs 5 and 6 considerable seed was secured, but it appears that fertilization was reduced by removal of the styles at this stage. In the last 4 pairs there is no larger difference between treated and check plants than would be expected of plants within the same strain, except in the case of pair 9. It is worthy of note, however, that while the styles were removed from the treated plant of this pair when they showed what appeared to be a definite recession, this stage occurred very early in the day, as compared with the other plant which was treated at the same stage. Thus it appears this plant was somewhat unusual, and too much consideration should not be given to it in drawing conclusions.

TABLE 2.—RESULTS OF STUDY OF POLLEN TUBE PENETRATION OF STYLE

Pair No.	Percentage seed setting		Treatment	
	Treated	Check	Time	Stage of removal of styles
	%	%		
1	0.02	83.9	7.30 a.m.	Pollen emerging from anthers.
2	0.00	78.1	7.30 a.m.	Pollen emerging from anthers.
3	4.5	51.4	5.00 p.m.	Stigmas emerged from anthers.
4	1.2	78.1	6.00 p.m.	Stigmas emerged from anthers.
5	37.9	60.5	8.00 a.m.	Stigmas divided and turning back.
6	52.4	71.1	8.00 a.m.	Stigmas divided and turning back.
7	55.6	56.4	10.00 a.m.	Stigmas turned back and receding.
8	51.8	52.4	11.00 a.m.	Stigmas turned back and receding.
9	38.7	53.9	10.00 a.m.	Stigmas showing a definite recession.
10	66.3	78.1	5.00 p.m.	Stigmas showing a definite recession.

Considering the results from this study and the previously described pollen germination study, it can be concluded that while germinating pollen grains are found on the stigmas in the evening of the same day that a flower opens, in very few cases has pollen tube penetration proceeded far enough to release the gametes and permit fertilization of the ovary. Early the following morning, by which time the stigmas are divided and turned back, the pollen tubes have penetrated sufficiently for fertilization to occur in many cases, but there is a large number of ovules in which this is not so. By the time the stigmas have started to recede in the late forenoon the pollen tubes have penetrated far enough to permit fertilization of the normal number of ovules.

MODE OF POLLINATION

A study was conducted in 1939 to determine if wind is an important factor in the transport of sunflower pollen. Sets of 8 microscope slides lightly smeared with vaseline were exposed under various conditions in the sunflower nursery during the flowering period. One slide was placed in a small tin clip mounted on a vane at each of the following heights: 2, 4, 6, and 8 feet. With this mounting the greased surface was always held into the wind in a vertical position. Another set of 4 slides was placed at the same heights in a fixed horizontal position. Two similar groups were set up in a block of crested wheat grass and brome grass plots, in order to obtain comparative data from crops which were known to be wind pollinated. These slides were removed every second day, and the number of pollen grains of the crop concerned counted for 5 random microscope fields. A low-power field of approximately 1.35 mm. in diameter was counted. In some cases the pollen was so abundant it was impossible to count a low-power field. In such cases a high-power field was counted and converted to terms of a low-power field. The data secured in this study are summarized in Table 3.

The outstanding feature of Table 3 noticeable in all comparative cases is the much larger number of grains secured in the case of grass pollen which is wind borne. Furthermore, the grass pollen which, for the most part was released at heights of about 2 feet, was caught in the greatest quantity at the 4-foot level with a vertical slide, showing that the pollen of a wind-pollinated crop is buoyant and is carried upward into the air. In the case of the sunflower pollen which was released about 1 foot higher than the grass pollen, the figure for the 4-foot vertical exposure is not much higher than that for the 2-foot exposure. This indicates that the sunflower pollen lacks the buoyancy of grass pollen, and is not transported by the wind to as great an extent. This contention is further supported by the figures from the horizontally exposed slides. Obviously, pollen caught on these slides would be largely falling pollen. It will be noted that the ratio between the 2- and 4-foot levels in the case of grass pollen is 2 : 1, and in the case of sunflower pollen 6 : 1, showing that sunflower pollen, even if it is released into the air, is not carried upwards by air currents to any extent but falls rapidly. A further indication that sunflower pollen is not normally wind-borne is the fact that it was frequently found in clumps of 5 or more grains, whereas the grass pollen was uniformly distributed over the slides in single grains.

TABLE 3.—SUMMARY OF DATA SECURED FROM POLLEN TRAPS

—	Vertical exposure height				Horizontal exposure height			
	2′	4′	6′	8′	2′	4′	6′	8′
Grass pollen Average number of grains per field	64.3	110.2	96.2	67.3	52.8	25.2	10.4	3.7
Sunflower pollen Average number of grains per field	3.05	3.74	1.92	0.75	5.71	0.89	0.17	0.14

Data collected from another study also support the conclusion that sunflowers are not highly wind pollinated. For the three years a number of heads were isolated in tiffany bags. These are open mesh bags which check large insects such as bees, but allow passage of wind-borne pollen. A summary of the percentage seed setting from heads under tiffany bags and paper bags, and from open-fertilized check plants is presented in Table 4. On the basis of the 3-year average, the percentage seed setting under tiffany bags is less than one-half of the open-fertilized check, and only 16% higher than the figure for paper bags. Such a condition indicates strongly that the sunflower is not wind pollinated to any large extent.

TABLE 4.—SUMMARY OF SEED SETTING SECURED UNDER TIFFANY AND PAPER BAGS AND ON OPEN FERTILIZED CHECK HEADS

Method of isolation	1937		1938		1939		Mean of 3 years
	No. of plants	Mean percentage seed setting	No. of plants	Mean percentage seed setting	No. of plants	Mean percentage seed setting	
		%		%		%	%
Tiffany bag	25	22.07	25	28.09	20	30.50	26.88
Paper bag	28	13.49	25	11.18	20	8.28	10.92
Check (open fertilized)	25	76.60	25	64.86	20	56.89	66.12

EXTENT OF NATURAL CROSSING

A number of uniform Ottawa inbred lines with contrasting morphological characters were grown in close proximity to each other in 1938. In 1939 progenies of 3 different lines with recessive characters were grown to obtain an estimate of the percentage of natural crossing.

The three lines showed 75.4, 50.0 and 78.1% of natural hybrids. Considering all plants in the study together the figure was 70.1%, which is a relatively high percentage natural crossing. As it has been shown that the pollen is largely not wind-borne, this crossing must be due to insects. The belief is supported by the fact that bees heavily loaded with pollen are frequent on the flowers.

PRELIMINARY GENETIC STUDIES

In 1937 a cross was made between 2 pure breeding inbred lines designated S-438 and S-439. Two contrasted pairs of morphological characters were involved. Line S-438 had a stem branching the full length except for the upper 3 or 4 leaves, and S-439 possessed a single stem. Line S-438 had black and gray striped seed (pigment in third layer), and S-439 had black and white striped seed (no pigment in third layer). Crosses were made in both directions. In 1938 the F_1 progeny, using line S-439 as the female parent, showed 80% of the plants with branching stem and seed with pigmented third layer. These were obviously hybrids and they were self-fertilized by isolating the heads with paper bags.

In 1939 four F_2 progenies, comprising a total of about 215 plants, were grown. Besides segregating in the 2 characters already mentioned, following the first fall frost in 1939 there was a segregation for frost

resistance. This frost which occurred on September 7 registered 29.7° F. at the University of Saskatchewan weather observation station. The temperature may not have been quite the same in the field nurseries which were almost a mile distant. In any case the frost was severe enough to kill the leaves on Gehu corn growing there. The leaves on the S-438 parent were also completely destroyed but those of the S-439 parent showed no noticeable damage. A summary of the behaviour of the three segregating characters is presented in Table 5. The lack of data for frost segregation in the case of the fourth progeny does not mean this progeny was not segregating. The absence of data in this case is an error of omission.

In Table 5 each pair of characters has been considered separately, then the combined behaviour of the seed and stem characters and finally the behaviour of all 3 pairs together. The Chi-square values and corresponding probability values for a test of goodness of fit to a 1-factor ratio for the separate characters, a 2-factor ratio for the seed and stem characters, and a 3-factor ratio for the combined characters all show close fits.

TABLE 5.—SUMMARY OF PLANT DESCRIPTION IN F_2 PROGENIES OF CROSS S-439 × S-438

Character*	Progeny No. 1	Progeny No. 2	Progeny No. 3	Progeny No. 4	Sum of all progenies
Br	43	52	39	33	167
Si	13	10	19	16	58
	X^2 for 3 : 1 ratio = .0725 P = .70 – .80				
Bg	38	39	43	35	155
Bw	16	16	15	13	60
	X^2 for 3 : 1 ratio = .9689 P = .30–.50				
FR	41	44	43	—	128
FS	16	17	16	—	49
	X^2 for 3 : 1 ratio = .6797 P = .30–.50				
Bg Br	28	35	27	23	113
Bg Si	8	4	15	12	39
Bw Br	14	12	11	9	46
Bw Si	3	3	4	4	14
	X^2 for 9 : 3 : 3 : 1 ratio = 1.3665 P = .70–.80				
Bg Br FR	20	26	18	—	64
Bg Br FS	8	9	9	—	26
Bg Si FR	4	4	12	—	20
Bg Si FS	2	0	3	—	5
Bw Br FR	10	7	8	—	25
Bw Br FS	4	6	3	—	13
Bw Si FR	2	3	2	—	7
Bw Si FS	1	0	1	—	2
	X^2 for 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1 ratio = 6.1802 P = .50–.70				

*S-439—Single stem (Si), Black and white striped seed (Bw), Frost resistant (FR).
S-438—Branching stem (Br), Black and gray striped seed (Bg), Frost susceptible (FS).

From these results it can be concluded that the differences in branching, colour of the innermost region of the seed coat and frost resistance in the 2 lines S-438 and S-439 are each dependent on a single genetic factor with a dominance of the branching character, pigmented condition of the innermost region of the seed coat and frost resistance. No linkage was found to exist between the 3 characters.

It should not, however, be concluded that similar results will be secured from crossing the same characters in other lines. The existence of a great range of branching types in the Mennonite material would indicate that the condition in this material is dependent on many more than one genetic factor. In the case of the pigmented undercoat, while no range of variations occurs as in branching, it is worthy of note that this condition, which was a dominant character in the cross studied, is far from being predominant in the lines of Mennonite origin.

SUMMARY

1. Observations of different types of plants with regard to stem type and stem strength are presented.

2. The existence of 3 separate coats in the sunflower seed, each apparently taking pigment entirely independent of the other 2, has been observed.

3. A description of the development of the sunflower head and of the individual flower during flowering is given.

4. Germinated pollen grains are frequently found on the stigmas the same day that the individual flowers open, but by means of other studies it has been shown that the pollen tubes do not reach the ovary in many flowers until the late forenoon of the following day.

5. The development of the individual flowers proceeds more rapidly on warm, clear days than on cool, overcast days.

6. By means of pollen traps and isolations with tiffany bags it has been shown that the sunflower is not highly wind pollinated.

7. Limited studies on the percentage of natural crossing indicate the figure is about 70% for sunflowers.

8. The dominance of vigorously branching character over single stem, pigmented seed undercoat over clear undercoat, and fall frost resistance over susceptibility, each dependent on a single factor with no linkage, is shown in the F_2 of a cross between 2 inbred lines.

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REFERENCES

1. Arnoldova, O. N. To the biology of sunflower blooming in connection with the technics of its crossing. J. Expt. Landw. Sudost. Eur. Russ. 3 : 131-143. 1926.

2. Cardon, P. V. Sunflower studies. J. Am. Soc. Agron. 14 : 69-72. 1922.

3. Cockerell, T. D. A. Suppression and loss of characters in sunflowers. Sci. n.s. 40 : 283-285. 1914.

4. Cockerell, T. D. A. Specific and varietal characters in annual sunflowers. Am. Nat. 49 : 609-622. 1915.

5. Hamilton, R. I. Improving sunflowers by inbreeding. Sci. Agr. 6 : 190-192. 1926.

6. Ross, A. M. Some morphological characters of *Helianthus annuus* L., and their relationship to the yield of seed and oil. Sci. Agr. 19 : 372-379. 1939.

7. Schiebe, A. Zuechtungs probleme bei Sonnen-blumen. Der Zuchter-10 Johrang, Heft 5 : 126-136. 1938.

8. Warner, Marjorie F. Sunflower *(Helianthus annuus)*. Bibliography. Agricultural library notes. V. 5, No. 1-3, Jan. to March 1930 Supplement. U.S. Dept. of Agric. Library. 1930.

The Library, Saskatchewan Department of Agriculture, Regina, Sask., is in need of copies of early volumes of *Scientific Agriculture*. Any person having spare copies for 1920, 1921, and 1922, and willing to donate them, may write to Mr. S. H. Vigor, Department of Agriculture, Regina, Sask.

THE IDENTIFICATION OF LIVE STOCK BY TATTOOING[1]

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Owners of small groups of animals kept as pets or for breeding purposes may be able to recognize certain individuals by natural markings or characteristics, but for positive identification a distinguishing mark or label is required. The necessity of individual identification is self evident in a large group of animals or where it concerns the registration of pure bred live stock, the transfer of ownership, and for breeding and progeny records.

In Canada, various live stock associations have adopted definite methods of identifying animals for registration purposes; these have subsequently been accepted by regulation as complying with the provisions of the Live Stock Pedigree Act. For some years certain breeds of live stock have been registered where the accepted method of individual identification is tattooing. Of the 28 breed associations whose records are maintained by the Canadian National Live Stock Records, tattooing for registration purposes is compulsory for 6 breeds of cattle and 2 breeds of swine, as well as for goats and silver foxes. In addition, tattooing is one of the alternative accepted methods of identification for dogs, poultry, sheep, 4 breeds of cattle, and some swine breeds.

The extension of tattooing to include other breeds of animals has been retarded because of its reputed inadequacy in some cases. The project here reported was initiated by the Production Service of the Dominion Department of Agriculture in an effort to secure data on the cause of reported difficulties and complaints. Considerable time has been spent in the collection of data, making observations at intervals on a large number of individual animals, and the compounding of many experimental pigment mixtures. In spite of sustained effort and the active co-operation of a number of individuals it must be admitted that all of the problems encountered have not been completely solved, but it is thought that the information given will be of interest to breeders and to agricultural workers generally and will indicate lines for further investigation.

METHODS OF ANIMAL IDENTIFICATION

It is axiomatic that the maintenance of blood lines requires the registration of parents and progeny, and registration is effective only where a practical and positive method of individual animal identification is provided. A satisfactory method must be reasonably permanent, relatively painless, and must not involve either mutilation of the animal or toxic effects. Methods that have been proposed, some of which have been successfully applied, include ear tagging, tattooing, chemical and heat branding, nose printing, photography, and colour charting.

Obviously, some of these methods are unsuitable for certain animals. For instance, photography would not supply identification for solid

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coloured animals, nor would colour charting be practical for poultry, nor could nose printing be recommended for swine. The latter method has been used by some dog breeders. Opinions have been expressed that in Canada this method is of doubtful utility, because of the fact that there is difficulty in making positive identification of a subsequent print with the original. In any case a new nose print is required on each occasion when it is necessary to establish the animal's identity. Nose printing of dogs is not condemned, but it is felt that until further work proves its practicability, it cannot be considered infallible in the hands of the average dog breeder.

While most of the methods enumerated have definite merit, if properly applied, the emphasis here is placed on tattooing, with a passing reference to ear tagging. To take care of contingencies, both of these methods may be used to make identification certain in some cases. The suggestions made are based on observations rather than preconceived opinions.

Ear Tagging

Metal ear tags are reasonably cheap, readily applied and easily deciphered, and can be recommended where applicable, and if necessary, in conjunction with other methods. Reference is made to this in a later section. Probably the greatest objection to the use of ear tags alone for positive identification, is that they may be torn out by contact with wire fences, undergrowth, etc., or removed. The great advantage of a tag is its readability. There is available in Canada a tamper-proof tag, which, when forcibly removed, results in its alteration and so prevents illegal use in another animal. The use of ear tags is so widespread that little comment need be made except to say that when placed in the ears of young animals sufficient space should be allowed for subsequent growth, to avoid creasing.

Tattooing

Tattooing has been practised by breeders of Yorkshire and Chester White Swine, Brown swiss, Canadian, Guernsey, Jersey, Hereford and Red Poll cattle, silver foxes, and goats. The associations of these breeders accept tattooing as the only means of identification. As mentioned above, individual breeders of other animals also use tattooing, which in the main has been satisfactory.

During the course of this investigation animals other than those already mentioned have been successfully tattooed, and some of the causes of complaints which have created prejudice have been discovered.

The pigment mixture in general use is a modified India ink, the colouring matter of which is carbon. Carbon black is condensed smoke, which makes available a pigment which is colloidal in particle size, jet black in shade, and high adsorptive capacity. The quality of carbon used is important and is reflected in the ink. The higher grades of carbon yield the best results.

While the chemistry of carbon includes hundreds of compounds, the element has no disposition to unite with living tissue or the blood stream. Thus when used in a tattoo mixture it does not deteriorate, or cause toxic

effects, being unique in this respect. It provides an ideal substance for producing a mark in contrast to flesh, even where brown pigmentation occurs. When the skin pigmentation shows deep shades of brown, approaching black, carbon tattoo marks can be still deciphered, especially with the aid of transmitted light. Incidentally, in all the animals examined no really black skin was noted and certainly none with the depth of colour of carbon, though often hair growth is intensely black.

To intensify the depth of colour and to increase the ease of reading black tattoo marks, a concentrated form of carbon pigment has been developed, in the form of a paste, which is now available.

Good workmanship demands that proper materials and proper technique be employed. Apropos the correct technique, an instance is known where, in tattooing a calf, the needle punctures were correctly placed on the inside of the ear but the ink was applied to the *outside*. In another case, ordinary writing ink was used instead of a proper tattoo pigment. The results in both cases were naturally somewhat less than satisfactory.

The tattooing of an animal, while not as speedily accomplished as ear tagging, is nevertheless reasonably simple and is effective if properly done. Improper technique invites failure and dissatisfaction. Mature animals can be tattooed successfully but, in general, animals should be marked when young, the opportune time in most cases being weaning time or even sooner. At this age the skin is soft and pliable, hair growth is usually sparse, the animal is more easily handled, and because of the animal's subsequent growth the tattoo becomes greatly enlarged and consequently more readable. An additional advantage is that a young animal heals quickly.

Correct Technique

The proper size of tattoo pliers to be used is regulated by the size of the animal and the area to be tattooed.

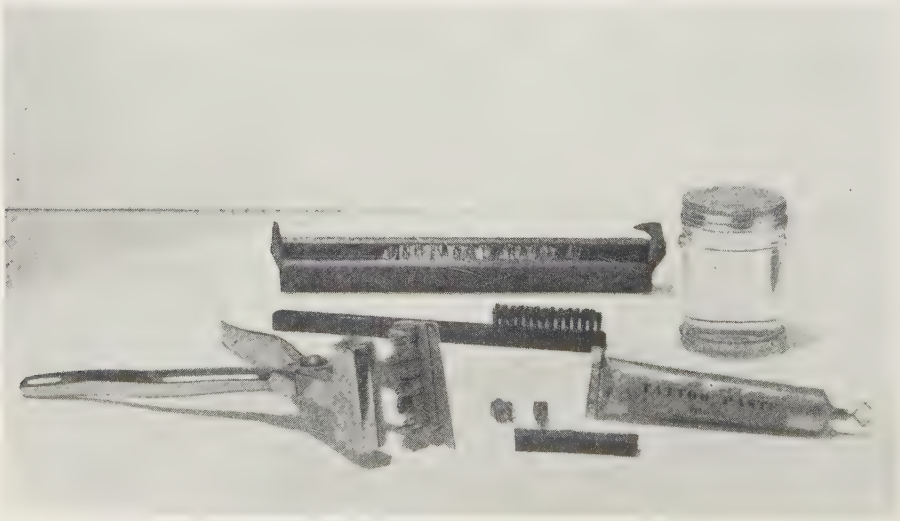

FIGURE 1. Typical tattoo kit, showing pliers, box of dies, cleaning fluid, stripping pad, tube of paste and brush.

FIGURE 2. Pocket pen light for tattoo examination.

1. Insert the correct symbols in the pliers and press down very firmly over the needles a thin rubber sponge pad. This pad helps to release the needles from the skin.

2. Check the correctness of the symbols by making a mark on a piece of paper.

3. Halter or muzzle the animal, if necessary.

4. Cleanse the area to be tattooed, using a cloth dampened with carbon tetrachloride, alcohol, gasoline or kerosene to remove, dirt, grease, and wax. One of the advantages of carbon tetrachloride is that it is non-inflammable. Any of these fluids may usually be purchased locally or from the manufacturers of tattooing equipment. In lip tattooing no cleaning is needed.

5. Smear pigment on the needles and on the skin, choosing an area free from freckles and warts if possible. If the tattoo is to be made on the ears, place the symbols parallel to and between the veins or cartilagenous ridges. The accidental piercing of a vein vitiates the tattoo.

6. Make the imprint with a quick firm movement and immediately apply a further amount of pigment from the container on the tattoo and rub vigorously and continuously for at least fifteen seconds to ensure penetration. *This is important.* The most effective method is to rub with thumb and forefinger, though a brush may be used.

7. Remove the rubber pad and rinse it and the needles in water, then dry. The sponge rubber pad should be discarded when it begins to lose its elasticity. The brush, if one is used, should also be rinsed.

8. Do not disturb the area until the healing process is complete, which may be from 5 days to 21 days, depending on the age and breed of the animal.

A typical tattoo kit is shown in Figure 1.

The type and quality of pigment used is a prime consideration. If, inadvertently, the cap of a pigment container is left off for a considerable

time, the volatile ingredients escape, leaving a thick residue. This residue should never be diluted with water. Good materials are essential and it is better to discard doubtful pigment than to invite disappointing results.

Examination of Tattoos

There have been some complaints that no matter how carefully the tattooing was done, it was difficult or impossible at a later date to decipher the symbols. On dark eared animals, and here the reference is to the skin and not the hair growth, it is true that when viewed by reflected light identification is sometimes not easy.

In some cases observed, a simple cleaning of the tattooed surface was all that was necessary; in others, the aid of a light behind the area was required. It may be mentioned here that the ordinary flashlight is not nearly as efficient as a vest pocket pen light having a short focus bulb (Figure 2). The light should be pressed firmly against the flesh opposite the tattoo, when the symbols may be viewed against the light shining through the surrounding tissue. Examination by transmitted light is more easily accomplished in a shed than outdoors. Occasionally it may be necessary to remove excessive hair growth before making an inspection.

The above suggestions will, in many cases, make it possible to decipher a tattoo mark which might otherwise be thought illegible. It is recommended that where tattooing is not now restricted by regulation to specific areas, the tattoo be placed on the animal where the skin is lightest in colour, in order to obtain the greatest possible contrast.

Coloured Tattoo Inks

In response to a reported need, efforts were made to develop a coloured tattoo mixture which would meet the requirements for brilliancy, permanency, and non-toxicity. So far these efforts have been unsuccessful: 46 different formulae have been tested on various kinds of animals ranging in size from guinea pigs to cows. The colour mediums tested included metals, metallic salts, clay, and different types of dyestuffs. Among the metals and salts tested may be mentioned aluminum, mercuric and cadmium sulphides, and titanium dioxide.

The action of different kinds and amounts of blood coagulants, astringents and protective coatings, including tannic acid, hydrastis, epinephrine and alum solutions has also been studied, in an attempt to correlate the extent of bleeding consequent to tattooing with the efficiency of pigment mixtures.

One hundred and one animals of different breeds have been used in the tests on coloured pigments, the trial tattoos on these test animals numbering over 200. Frequent inspections were necessary to follow the

FIGURE 3. Facsimile of tattoo dies, illustrating the range of sizes available. Both needle and chisel points are shown.

progress of any one formula, which involved the keeping of a detailed file for each animal. The observations on an experimental tattoo necessarily extended over a period of months, so that the investigation to date has occupied a considerable period of time.

Such factors as the age of animals, the size and type of tattoo pliers and needles, and variations in technique of application of coloured inks were also studied.

That a completely satisfactory coloured ink cannot yet be offered is a disappointment, because there are cases where, if such were available, identification of tattoos could be more easily accomplished than at present. This applies particularly to large animals which present difficulty in handling.

To illustrate the difficulty of adapting a pigment for tattoo purposes, the case of titanium dioxide may be given. This material is widely used in white paints and is considered quite fast to light and has good resistance to weathering effects. (Lead oxide, used also in white paint, was not tried, of course, because of its known poisonous effect.) Titanium apparently combines with some element in the blood stream or tissues because, although while tattoos in animals at first gave great promise and were distinct enough to photograph, they showed rapid deterioration at the end of seven to eight weeks. These tattoos merged into the background and were eventually almost indistinguishable. Other pigments which showed less tendency to fade did not, however, provide sufficient brilliance or depth of colour to be satisfactory.

It is contended that the number of cases where a coloured pigment is absolutely essential for tattooing purposes is extremely limited, and until such time as a satisfactory one is developed or discovered, carbon inks and pastes should give identification in the vast majority of cases. It is inferred, of course, that care is taken both in the making and in the examination of tattooes. While to date no coloured pigment that is completely satisfactory is available for easy identification on very dark skin, some of the formulae have distinct possibilities, for instance, in the case of certain breeds of sheep, where fading of black tattooes has been experienced. Reference is made to this later in the report.

Berkshire Swine

The practicability of tattooing this breed having been questioned, it was decided to secure a cross-section of opinion of registered breeders and owners, to determine the extent of tattooing and if difficulties had been encountered.

Of the 72 registered breeders and owners to whom a questionnaire was sent, 50% responded. Information was asked with respect to the type of tattoo pliers, nature of pigment mixture, age of swine at tattooing, difficulty of deciphering symbols, signs of infection, etc. Apparently tattooing of this breed is not widely practised, since nearly thirty of those circularized reported no experience.

The opinions expressed are of interest, the following quotations being typical: "Told it does not stay on black pigs"; "would like to know more about tattooing"; "do not see how black pigs can be tattooed, unless

with red or white ink"; "tattooing is the best method of identification, as it is impossible to change the pedigree"; "ear tag is much cheaper and simpler"; "hard to read in black pigs especially when oiled at show time"; "tags fairly satisfactory, though lost occasionally". Of those who have tried tattooing, none is completely satisfied with the present facilities, mainly because of the difficulty of reading the tattoo symbol.

Experimental Data for Berkshire Swine

Because of the lack of Berkshire swine in the Ottawa district, the trials were rather restricted and while some conclusions can be drawn from the data secured, an experiment involving a much larger number of animals would have been more satisfactory. Through the co-operation of four Ottawa Valley farmers, 20 pigs in the age groups, 3 weeks, 2, 3 and 4 months, and one boar aged 2 years were made available for tests. It was found possible to keep a number of these under observation for a period of 5 months.

The tattoo pigments used were black paste, black ink, and a red paste. To eliminate the personal factor, all the tattooing was done by one person, on the inside surfaces of both ears of each animal.

As the readability of a tattoo depends on contrast, observations were made on the pigmentation of the ears. Great variations were noted. Generally the colour of the outside ear was darker than the inside. In the pigs under test the pigmentation varied from a very light brown colour to very dark brown shades. Although the bristles are black, no skin that could properly be described as black was noted. Both ears of the same animal seldom had the same colouring. Frequently pale yellow or ivory coloured areas were seen. It is conceded that there may be Berkshire pigs with black skin, but none was observed in the animals tested.

In the test group there were only 2 illegible marks and in one of these poor results were expected because of insufficient application of ink due to the difficulty of holding the animal. Age may have been a contributing factor also. In the other case there was an unexplained diffusion of pigment mixture which caused a blurring of the tattoo. Incidentally a pig at market weight is not the easiest animal to handle and examine, and it was found convenient, if not essential, when tattooing as well as in subsequent examination, to have 3 persons available.

Observations at the end of 1 month indicated that the black paste was superior to the ink, but in the final assessment good tattoos were obtained with both types of pigment mixtures. The red paste was unsatisfactory, being very difficult to read, and white inks, by tests on other animals, were also found to be impractical. A thorough cleaning of the tattooed surface was found necessary in some cases and occasionally a pocket pen light similar to the kind shown in Figure 2 was used.

There has been no opportunity to check the possible deleterious effects of continued sunlight on Berkshire tattoos, a condition which occurs in Yorkshire swine. Sun scalds and blistering are usually soon corrected when the animal is stabled.

Recommendations for Berkshire Swine

It is suggested that in marking Berkshires, the area lightest in colour on the inside of the ears should be chosen. The technique as described

should be followed, with particular care taken to thoroughly rub the pigment into the needle punctures, especially if bleeding is excessive. Weaning time is considered opportune. The symbols used should be of the approximate dimensions, 11/32 inch high and $\frac{1}{4}$ inch wide, though a slightly larger size may also be used. These dimensions refer to the outline formed by the needles, which should have chisel points. Either black paste or black ink of good quality may be used.

Based on the experiments outlined, it is felt that most of the complaints with respect to the reading of Berkshire tattoos have probably been due to lack of care in placing the tattoo and the difficulty in securing the animal for making a careful examination.

In the case of extremely dark ears, tags can be usefully employed for quick identification, always keeping in mind that a tag may be lost, but a tattoo remains with the animal.

Clydesdale Horses

While range horses have for years been identified by heat branding, and chemical branding has been used to a lesser extent, objections have been raised in some sections of the country to both methods. Hoof marking is not permanent, there being a need for renewal at approximately 6 month intervals. Tattooing of the gums of horses is another method, which should be permanent for the life of the horse, if the correct pigment is used.

Some promising experiments have been made in a different area of the horse's mouth, namely, the inside surface of the lower lip, which, with some modifications of technique and equipment, can be made available. So far only the Clydesdale breed has been investigated, but the findings should be applicable to all breeds. Nearly 2 dozen horses were tested and the opportunity was taken to compare the efficiency of various sizes and shapes of tattoo pliers and needles, pigment mixtures, astringent solutions and protective coatings.

Tattooing Technique for Horses

All tattooing was done after the application of a twitch to the upper lip, and no particular difficulty was experienced. Instead of cleaning the area as in ear tattooing, the lip was wiped free of saliva. The pigment mixture, in this case carbon pastes and inks, was then quickly placed on the skin and on the needles. A rubber stripping pad for quick release was used and the lip held away from the teeth and gums to allow the pigment to set, after being thoroughly rubbed into the punctures.

Experimental Data for Horses

The enormous amount of saliva secreted by a horse, reported to be about 10 gallons per 24 hours, according to '*The Physiology of Domestic Animals*'—*Dukes*, was thought to be a factor in some of the tests. The necessary handling of the mouth tends also to increase the saliva flow. To minimize this effect, protective coatings of collodion and a special mixture having a nitrocotton base were applied.

The application of astringents, both as a solution brushed over the tattoo and incorporated in the tattoo formula, were of some assistance.

Very quick setting inks were also tested, but these gave mediocre results.

The location of the tattoo in the lip has some signficance, the side being found more suitable than the lower edge. In the latter place there is always the possibility of wounding and the consequent formation of scar tissue, due to piercing by stalks in the feed.

The effect of deep and shallow punctures was studied.

Summary for Horses

From the somewhat limited tests, which included horses up to 11 years of age, kept under inspection for a period of over 6 months, there is evidence to indicate the proper method for successful tattooing.

Special deep throated pliers and dies with a comparatively large number of needles of medium diameter and length are indicated. Used with a rubber stripping pad and the newly developed carbon paste this equipment warrants extended trials on horses of different breeds. For sharp definition in deciphering tattoos, transmitted light is valuable.

There is little, if any, disturbance caused by lip tattooing because mouth injuries heal quickly. It should be possible to tattoo foals easily, after weaning. Unfortunately, no horses of this age were available for these experiments.

The suggested location for the tattoo affords easy inspection.

Sheep

The registration of lambs identified either by ear tags or tattoo marks is accepted by the Canadian Sheep Breeders Association. Neither method has given complete satisfaction for all breeds, the former because of the occasional loss of tags and the latter because of illegibility after a period of years in some breeds, notably Southdown and Shropshire.

The legibility of sheep tattooes in the two breeds mentioned was the subject of investigation as well as the feasability of using black tattoos for Suffolk lambs.

Legibility of Shropshire Tattoos

A flock of tattooed Shropshire sheep, composed of 63 animals ranging in age from 1 to 9 years, was thoroughly examined. The examination was conducted as follows:—

Identification was first attempted without cleaning the ears, followed if necessary by wiping with a cloth dampened with carbon tetrachloride, to remove grease and wax. If after this treatment the tattoo was still undecipherable, a pocket pen light was held behind the tattoo. The data are submitted in Table 1.

Table 1.—Legibility of Shropshire Tattoos

Age of Tattoo Years	Number of Tattoos	Legibility without cleaning	Legibility after cleaning	Legibility with transmitted light
		%	%	%
1	24	96	96	96
2	39	56	66	74
3	4	50	50	50
4	24	50	66	66
5	22	17	17	22
6	6	0	0	16
7	2	0	0	0
8	2	0	0	0

These data indicate that, in this flock, the percentage of legible marks drops quickly after 4 years, which is an unsatisfactory condition. Even 2-year markings cannot be considered ideal, and this in a flock where it is known the tattooing was carefully done. Incidentally, in this flock where ear tags are used as a double safeguard, remarkably few tags were lost.

The pigment mixture used in the above sheep was a black ink of the type in general use. In an experiment recently commenced, there is some evidence that paste tattoos may effect some improvement.

Southdown Sheep

Some Southdown tattoos have been examined and evidence was found that the pigmented areas frequently block out portions of tattoo symbols. These coloured areas appear only as freckles in a young lamb, but as the animal matures, grow into larger patches which are frequently quite dark in colour. No tabulation of the legibility of Southdown tattoo marks was made, but observations indicate that tattooing is not always satisfactory.

Suffolk Sheep

A group of lambs of this breed was used in comparing the efficiency of black ink and paste tattoos. Nine lambs were marked in both ears and at the end of 4 months there was no difficulty in making identification. The paste tattoos gave noticeably darker marks than the ink.

Lambs marked at 6 weeks of age had better marks than those marked at 1 week, due apparently to a thinning out of the pigment on account of ear growth.

In this breed, although the hair growth on the ears is undoubtedly black, the skin of the lamb's ear varies in colour from flesh pink to dark brown. There are relatively large freckled areas.

The examination of older tattooed marks would not be expected to give difficulty, especially when using transmitted light, although no adult animals have been inspected. There has been no opportunity to check the possible fading of tattoos over a period of years.

Coloured Pigments

While numerous coloured tattoo mixtures have so far failed to give contrasting shades to dark skin, some of them do give promise of success for Southdown and Shropshire sheep in overcoming the difficulty mentioned with pigmented areas.

A small experimental group of Shropshire sheep showed excellent coloured tattoos at the end of 7 months. One of the pigments under trial is known as Monastral Fast Blue BS, a dyestuff whose constitution is similar to that of haemin, the colouring matter of blood. This dyestuff shows properties of fastness to light, acids and alkalis and no welting was caused by this pigment, an effect often caused by other pigments. The blue formula with 2 other colours, which in preliminary trials also showed promise, are now the subject of study by 3 different institutions. Sheep of different breeds will be kept under observation for at least 3 years to determine the permanence and readability of coloured tattoos.

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Conclusions for Sheep

With respect to the identification of sheep in those breeds which have been checked and where difficulty has been experienced, it would seem wise to anticipate all contingencies by employing both ear tags and tattoos. There remains the possibility that an animal in a flock may, after a period of years, carry an undecipherable mark and may also have lost its tag, but this circumstance is improbable. It should be emphasized that the fading of black tattoos is mainly the concern of a breeder who carries pure bred stock for a period of years and then transfers ownership.

The disappearance of carbon tattoos is peculiar to sheep and is thought to be due to a thickening of the ear tissues, rather than to a diffusion of carbon in the tissues. A long test period is needed to determine if the more concentrated paste or one of the coloured pigments will furnish satisfactory identification.

Cattle

The tattooing of cattle is on a well established basis and has been practised for many years. It is compulsory for some breeds, but optional for others. In general, tattooing has been satisfactory, but in certain cases has been the cause of some complaints. An attempt has been made to improve tattooing facilities.

Experiments were conducted (1) to test the superiority of carbon pastes over the black inks in general use, (2) to test the feasibility of tattooing breeds not as yet so identified, by the use of both black and coloured inks. The test animals were Ayrshire calves, Holstein-Friesian and Aberdeen-Angus cattle.

Improved Tattoo Paste

A number of Ayrshire calves tattooed in some cases with paste and in others with ink were kept under inspection for 5 months.

Better tattoos resulted when the animals were marked at 1 month of age than when 10 days old. The paste tattoos were very definitely superior to those where the thinner ink was used. While all tattoos in the group were legible, the increase in depth of colour and clear cut margins in the paste tattoos were marked.

With respect to the pigment, these tests are conclusive, though limited in scope. The optimum age for tattooing is not indicated here, but tattooing should apparently not be done before one month of age.

Holstein-Friesian Cattle

Seven coloured pigments, as well as carbon ink, were tested on animals from 1 to 8 years old. There were 27 animals in the group and the observation period was for 9 months, although not all tests could be followed through to the end of the period.

The results were disappointing in that only a small percentage of tattoos were legible. None of the coloured marks approached the standard required and few of the black tattoos were readable.

However, before condemning tattooing for this breed, larger scale trials should be arranged. No Holstein calves were tattooed, and experience with other animals has shown that success is more certain when young

stock is marked. It is thought that with special deep-throated pliers the tattoo can be placed well in toward the base of the ear. This area is usually light in colour and even at maturity is free from hair. The outer margins of Holstein ears are frequently rather heavily pigmented and hairy, conditions which hinder tattoo identification. The carbon paste and one of the light coloured inks now being tested on sheep could with advantage be tested on a wider scale.

Incidentally, following summer pasturing there was a noticeable increase of ear pigmentation. No infection or disfigurement was seen in or around the tattoo sites.

FIGURE 4. Tattooing of Ayrshire calf.

Aberdeen-Angus Cattle

Because of the scarcity of this breed in the vicinity, experimental tattooing trials were very limited.

One herd was visited and 5 animals were selected for tests. A bull and some calves were examined, these had a rather sparse growth of hair in the ears, which was in contrast to cows recently brought in from the range. While the hair is black the colouring of the skin on the inside of the ears is dark ivory, and offers a good contrast to black pigments.

The test animals were slaughtered 6 weeks after tattooing and the ears secured for a critical examination. The test period was of very short duration, but sufficiently long to demonstrate that aluminum, kaolin and titanium dioxide pigments are useless. On the other hand, both carbon ink and paste provided legible tattoos.

Summary for Cattle

Carbon paste can be recommended as being superior to carbon ink for tattooing Ayrshire calves.

Although the trials with Holsteins were inconclusive, further investigation along the lines suggested is expected to demonstrate the feasibility of tattooing for this breed.

The tattooing of Aberdeen-Angus calves should offer no particular difficulty, although subsequent examination of mature animals might require the clipping of hair over the tattooed area.

There appears to be no correlation between the amount of bleeding caused by the tattooing operation and legibility of tattoo. Temporary blanching of the site of the tattoo with injections of epinephrine solutions was of doubtful utility.

The growth of warts on the ears of cattle sometimes renders tattoo marks illegible. This contingency may be anticipated by the use of an ear tag.

For calf tattooing the symbol size should be approximately 11/32 inch high and $\frac{1}{4}$ inch wide. A larger size may be used for mature cattle.

Dogs

There appears to be a difference of opinion among dog breeders with respect to tattooing, but in general, breeders who approve of and practise tattooing have had satisfactory results. Some breeders report failure or only partial success, while others refuse outright to consider this method of identification. On the other hand, there are staunch advocates of dog tattooing.

Objections have been raised to the practice of dog tattooing because of the pain involved. The reactions of puppies have been observed immediately following tattooing and invariably normal behaviour was noted. Undoubtedly, since tattooing is accomplished so quickly, pain is only momentary. In any event, no one could compare the distress caused to a dog by tattooing with either ear cropping or tail docking, which in some breeds appear to be regular practice.

The prime consideration in any system of identification should be permanence and reliability and the tattooing of dogs has been approached from that viewpoint. An extensive survey has been made of the possibilities and limitations of tattooing as a positive method of dog indentification.

Extent of Survey

It can be said at the outset that one of the chief objects of the investigation was to develop a coloured tattoo mixture for use on dark skinned

dogs that would compare favourably with black tattoo marks on flesh coloured skin in permanence and legibility. No such pigment mixture can yet be recommended, although very extensive trials have been made, employing different breeds and ages of dogs, pigment mixtures and sizes of tattoo pliers.

To indicate the efforts made, it may be recorded that during the course of this investigation, which occupied 10 months, 33 different non-toxic pigment mixtures were tested on dogs, 4 different sizes of tattoo dies were used, and 168 separate tattoos were made; 391 inspections of these marks were required, which involved the keeping of an individual file for each animal.

Carbon inks, as pointed out previously, provide an ideal medium for tattooing and, in view of the negative findings with coloured pigments and believing that tattooing as a means of identification is superior to alternative methods, a critical examination of a number of breeds of dogs was made. The purpose of this examination was to determine suitable locations where carbon base inks could be used effectively.

No dog was observed that did not have some area of skin surface which would provide a contrast to black pigment. In some breeds these locations may not be considered ideal, because of a heavy coat or due to difficulties in handling or in making subsequent examination.

There is nothing in the constitution of the Canadian Kennel Club restricting areas that may be tattooed for registration purposes. As different breeds differ widely in skin coloration (even litter mates will not necessarily have the same pigmentation), different locations may logically be chosen by a breeder to achieve the best effect and the tattoos so registered.

Lip Tattooing of Dogs

There are, it is thought, very few dogs having the inner surface of the lips so dark that a jet black tattoo could not be deciphered, especially with the aid of transmitted light. The placing of a tattoo in this location is accomplished with the same equipment and with no more difficulty than elsewhere. A Canadian manufacturer has recently developed a small tattoo set which can advantageously be used for short-lipped breeds. Most dogs can, however, be tattooed in the lip with the tattoo pliers now on the market.

The arguments in favour of lip tattooing are concisely stated in the following quotations taken from a private communication—"less painful than the ear or any other skin surface"; "the mouth does not require the application of antiseptics"; "it is easily available and easily applied"; "the lining of the mouth is always clean, no hairs to obstruct the view and the tattoo marks are easily seen at a moment's notice"; "the marks are hidden from view"; "there is practically no danger of infection"; "salivation cannot possibly have any effect on this tattooing"; "as contrasted with nose prints and charts, this marking is always present and goes with him wherever he journeys"; "no deformity follows".

Lip tattooing has been investigated and favourable results obtained. It could be adopted with satisfaction by a great many dog breeders.

FIGURE 5. Lip tattoo (Fox Terrier). The symbol in the photograph is shown upside down. Larger dogs can be tattooed in the lower lip.

Flank and Belly Tattooing for Dogs

The loose skin on the upper flanks or the skin on the lower abdominal areas may be utilized for tattoos. Usually in puppies and in quite a number of breeds at maturity, the growth of hair is, in these areas, rather sparse. Even in those breeds which at maturity have heavy coats, identification is possible by clipping the hair over the tattoo.

There is no special difficulty in tattooing in the locations mentioned. It is essential to have an assistant to hold the fold of skin straight during the marking to prevent distortion of the symbols. The usual vigorous rubbing in of pigment should be practised here as in all cases. Some dogs have been satisfactorily marked in a standing position, but to ensure a careful job it is advisable to place the dog on its side or back.

The skin on a puppy expands rapidly and causes a considerable enlargement of the tattoo, and consequently small dies may be used. Although most of the observed tattoos on bellies and flanks were quite legible, one or two were noted showing a tendency for diffusion of pigment, giving a blurred outline to the tattoo symbol. For most breeds these areas are considered to be less favourable than either lips or ears.

Ear Tattooing for Dogs

Probably more dogs have been tattooed in the ears than in any other place, and few comments are necessary.

Opinions have been expressed that ear tattooing will change the carriage of a dog's ear, and conceivably in some breeds, careless workmanship might have this effect. Contrary opinions to this view have also been given.

It can be stated that none of the dogs under test showed any change in ear carriage and no deformities developed. Care should of course be taken to avoid piercing cartilagenous ridges.

Occasionally moderate bleeding is caused, due to the sometimes unavoidable puncturing of small blood vessels. This, of course, causes no harm to the dog, but it is a good practice in such cases to make a second application of pigment to the tattoo area to ensure good marking. The pigment mixture checks the tendency to bleed.

Suggested Tattoo Locations for Dogs

The following list, while admittedly not covering by any means all recognized breeds, suggests some locations that are considered suitable for black tattoos. These notes were compiled following the critical exam-

FIGURE 6. Details of lip tattoo shown in Fig. 5.

ination of a large number of dogs. It should be repeated that dogs show a great variation in skin pigmentation, and the ideal location for one dog is not necessarily the same as for another one.

Afghans (ears, lips); Boston terriers (upper lip); Bull terriers (ears, lips, flanks); Cairn terriers (ears, lips, flanks); Chow Chows (ears, flanks, lips); Collies (ears, lips); Daschundes (ears, lips); Dalmatians (flanks, ears, lips); Doberman-Pinschers (lips); Fox terriers—smooth and wire (lips, ears, flanks); Great Danes (ears, lips); Kerry Blue terriers (upper lips, ears); Lakeland terriers (flanks, ears, lips); Newfoundlands (ears, front upper lips); Norwegian Elk Hounds (ears); Pekingeses (ears); St. Bernards (ears, lips); Schipperkes (lips, flanks, ears); Sealyham terriers (lips, ears, flanks); Setters English and Irish (ears, upper lips); Spaniels—Cocker and Springer (lips, ears); Skye terriers (lips, flanks); West Highland White terriers (ears, flanks, lips); Whippets (ears, flanks); Wolfhounds (lips, ears, flanks); Yorkshire terriers (flanks).

In most breeds of dogs there is a choice of location for tattooing, and the logical location is the best one. Black ink and paste can, in the vast majority of cases, if used intelligently and carefully, continue to be the medium for the identification of dogs.

There may be objections on the part of some exhibitors to the suggestion made involving the clipping of hair where it is necessary to make examination of a tattoo, because the dog's appearance might be adversely affected. It is contended that the establishment of a dog's identity should be considered of prime importance in the show ring or elsewhere and if this requires the clipping of a small area, such action should have no adverse influence in the awarding of points. Such treatment, of course, has only a temporary effect.

Tattooing Technique for Dogs

Dogs, like other animals, should be marked when young. The general technique of tattooing has been described and is applicable to dogs, except that in lip marking no cleaning fluid is necessary nor should be used. A convenient location for a lip tattoo is opposite the fang, and not too close to the gums. After tattooing, the lip should be held away from the teeth and gums until the pigment mixture dries. All tattoos should be left undisturbed until the healing process is complete.

The size of tattoo pliers and needles used are regulated by the breed of dog and the location of the tattoo, bearing in mind that the mark will enlarge with the animal's growth. The three smallest sizes of dies, as shown in Figure 3, may be used.

CONCLUSIONS

The chief consideration of every breeder of pure bred live stock should be the maintenance of blood lines, and one of the chief concerns of every purchaser of pure bred live stock should be the positive identification of a pedigreed animal. Consequently, only the best and most effective method of animal identification should be considered.

No coloured tattoo pigment has been found that meets the required standards for brilliancy, permanency, non-toxicity, and ease of application.

A carbon base paste has been developed which, in most of the tests reported, was an improvement over black inks.

The technique of tattooing is relatively simple but requires care. While not completely satisfactory, it is in most cases a valuable method of identification. Some of the complaints with respect to illegibility are due to carelessness in tattoo examination; other complaints are well founded.

The investigation points out further lines of work which might profitably be explored, employing larger numbers of animals than has so far been possible. The co-operation of breeders in large scale tests would be invaluable.

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The photographs shown were taken by Mr. C. Lovell, by kind permission of the Associate Director, Experimental Farms Service.

INTERGENERIC CROSSES BETWEEN *TRITICUM* AND *AGROPYRON*[1]

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INTRODUCTION

In the Northern Great Plains area attempts to secure stands of the adapted perennial cultivated grasses have frequently been unsuccessful. Probably one of the most common reasons for failure has been over-deep seeding of these crops, the seeds of which have only sufficient food reserves to support the seedlings through their penetration of a relatively shallow depth of soil. On the other hand, seedings made at the proper depth have frequently been unsuccessful due to rapid drying of the surface soil, and to wind erosion.

These difficulties are not encountered to the same extent in the cereal grain crops, largely because the larger kernel size makes deeper seeding practical. Although careful attention to such factors as time of seeding, soil preparation, and protective soil covering can reduce greatly the risks involved in seeding the grasses at a shallow depth, it seems logical to assume that a large-seeded perennial grass would greatly aid in solving the problem. A crop having the large kernel character of wheat combined with several characteristics obtainable in perennial grasses seemed desirable.

The discovery by Tzitzin (44) that certain species of *Agropyron* would cross with *Triticum* led to the suggestion that crosses of this type could be utilized to combine the desired wheat character with the perennial habit, winter hardiness, root type, and foliage characteristics of the *Agropyrons*. Although the objective of the Russian work with these crosses was a perennial wheat, Tzitzin (44) recognized the possibility of producing new forage grasses. As soon as the report of his work became available, a breeding program was started at the Dominion Forage Crops Laboratory, Saskatoon, Saskatchewan, directed towards the development of a large seeded forage crop. This paper presents the results of this project from its inception to date.

MATERIALS AND METHODS

The species of wheat used in crossings were as follows: diploid species, *Haynaldia villosa* (Schur), *T. monococcum* (L.); tetraploid species, *T. dicoccoides* (Korn), *T. dicoccum* (Schubler), *T. durum* (Desf.), *T. turgidum* (L.), *T. polonicum* (L.), *T. timopheevi* (Zhuk.), *T. pyramidale* (Perc.), *T. orientale* (Perc.); hexaploid species, *T. vulgare* (Host), *T. compactum* (Host), and *T. sphaerococcum* (Perc.). In the crossing program *T. vulgare* was represented by 10 different varieties, half of which were spring and the balance winter types; 2 varieties of *T. durum* were also used.

The *Agropyrons* used in crossing were as follows: diploid species (n = 7), *A. cristatum* (L.) Beauv.; tetraploid species, *A. pauciflorum*

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Summary of a thesis submitted to the Graduate School of the University of Minnesota, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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(Schivein.), *A. subsecundum* (Link) Hitchc., *A. junceum* (L.) Beauv.; hexaploid species, *A. glaucum* Roem. and Schult., *A. repens* (L.) Beauv.; octoploid species, *A. smithii* Rydb.; decaploid species, *A. elongatum* (Host); unknown chromosome number, *A. inerme* (Scribn. and Smith) Rydb., *A. trichophorum* (Link) Richt.

In making the crosses the wheats were generally used as female parents, principally because hybrid seeds and plants could then be readily identified, whereas in the reciprocal crosses the grass-like characteristics of the F_0 seed and F_1 plants made separation of selfs from hybrids almost impossible by visual examination. In general the emasculation and pollination procedure was the same as described by Hayes and Garber (15). Pollination was accomplished by breaking a whole or a portion of a ripe anther into each floret. Armstrong (4), and Johnson and McLennan (18) used sable hair brushes for applying the pollen. With this exception, the emasculation and pollination technique was the same as described by these latter authors (4, 18).

In backcrossing, the F_1 hybrids were usually used as the female parent. In F_1 hybrids it was found that the proportion of good pollen was generally very low, so there was very little likelihood of success in the reciprocal backcross.

The hybrid material was started in the greenhouse and transplanted to single plant nurseries in the field in early May. In 1938 and 1939 nurseries were established at the Dominion Experimental Station, Melfort, Saskatchewan, as well as at Saskatoon, Saskatchewan.

Except in backcrossing, no measures were taken to control pollination in the hybrids. There was no grass parental material and very little wheat close to the location of the hybrids. The leathery nature of the anthers of the hybrids and the high proportion of poor pollen probably would limit very greatly the amount of intercrossing amongst the hybrids. Thus it is assumed the amount of natural backcrossing or intercrossing was probably very low, and most of the seed setting was the result of self fertilization.

In the tabulation of all the data where means were used, weighted averages were calculated. This was done to avoid discrepancies arising from wide variations in plant numbers, etc., in different crosses and generations.

CROSSING RESULTS

In a crossing program involving *Triticum* species and varieties with *A. repens*, *A. subsecundum*, *A. smithii*, *A. cristatum*, *A. inerme*, and *A. junceum*, no hybrid seeds were obtained from 3044 wheat florets pollinated. In crosses between *Triticum* spp. × *A. trichophorum*, 2.4% of the 411 florets pollinated set seed. These results are in general agreement with those of Armstrong (4), Johnson (19), Tzitzin (44), and Wakar (61). However, Tzitzin (44), Lapin (26), Cicin (9), and Veruskin (53) reported that *A. junceum* crossed readily with wheat. Krasnjuk (21) stated that he had obtained one hybrid plant from a cross of *Secale cereale* with *A. cristatum*.

The results from crosses of wheat with *A. elongatum* and *A. glaucum* as male parents are given in Table 1. As far as possible, the accuracy of the classification of the seeds as hybrids has been checked by germinating the seeds and studying the seedling and mature plant characteristics. All selfs have been omitted from the table.

The data presented in Table 1 show that *A. glaucum* was crossed successfully with all species of wheat excepting *T. sphaerococcum*, and that *A. elongatum* crossed fairly readily with all wheat species excepting *T. monococcum*. Except for the failure to effect hybridization of *T. monococcum* with *A. elongatum* the data confirm the results reported by Tzitzin (44), Armstrong (4), Johnson (19), Lapin (26), Wakar (61), Cicin (9), Veruskin (53), Verushkine and Shechurdine (51), and Verushkine (52). Not infrequently, however, the crossing success has been reported to be higher than found in this investigation.

TABLE 1.—RESULTS OF CROSSES INVOLVING SPECIES AND VARIETIES OF *Triticum* WITH *A. elongatum* AND *A. glaucum*

Female parent	Male parent—*A. elongatum*			Male parent—*A. glaucum*		
	No. of florets pollinated	Percentage seed setting		No. of florets pollinated	Percentage seed setting	
		Av. %	Max. %		Av. %	Max. %
Diploid wheats × *Agropyron* spp.						
Haynaldia villosa	209	11.96	66.7	216	0.92	8.33
T. monococcum	175	0.0	—	—	—	—
Tetraploid wheats × *Agropyron* spp.						
T. dicoccoides	320	7.50	37.5	90	2.22	10.0
T. dicoccum	1360	30.74	94.4	274	9.49	46.2
T. durum—						
Mindum	988	9.82	86.7	468	11.11	38.9
Pelissier	1356	36.95	85.0	520	9.81	55.0
T. turgidum	332	22.59	75.0	394	4.82	18.8
T. polonicum	651	9.98	66.7	126	4.76	50.0
T. timopheevi	588	25.85	79.2	274	15.33	33.3
T. pyramidale	200	14.50	60.0	277	14.44	70.0
Total and average	5795	23.50		2423	9.82	
Hexaploid wheats × *Agropyron* spp.						
T. sphaerococcum	—	—	—	70	0.0	—
T. vulgare—						
Apex	453	13.25	50.0	431	1.39	25.0
Marquis	1355	6.57	45.0	560	4.82	66.7
Reward	492	4.27	30.0	100	0.0	—
Chinese	548	20.26	45.8	456	4.38	20.8
Hope	515	3.49	40.0	288	3.12	22.2
Karkov	351	15.38	80.0	520	15.58	55.0
Lutescens	136	8.82	25.0	60	1.67	2.8
Dawson	192	20.83	75.0	—	—	—
Minhardi	180	3.84	15.0	48	0.0	—
Minturki	—	—	—	288	1.04	8.32
T. compactum—						
Little Club	500	39.00	95.0	240	1.25	10.0
Total and average	4722	12.85		3061	4.90	
Grand total and average	10901	18.28		5700	6.84	

The results in crosses involving *T. monococcum* are at variance with those reported by Tzitzin (44). He reported 70.2% success in crosses between this species and *A. glaucum* and 4.0% where *A. elongatum* was the male parent. Johnson (19) failed to obtain viable seeds in crosses of this wheat species with *A. glaucum*. In view of the failure of Johnson (19) and the writer to secure viable hybrid seeds with the diploid wheat species, it is of interest to note that the diploid *Haynaldia villosa* crossed quite readily with the decaploid *A. elongatum*.

Irrespective of which grass was used as the male parent, the data in Table 1 show that the average success of crosses involving the tetraploid wheats was almost double that of the hexaploid wheat combinations. The introduction of the C. genom by the hexaploid wheat for some reason results in a lower compatibility. Similar results have been found by Tzitzin (44) and Armstrong (4).

Significant differences were observed between the compatibility of crosses of the grass species with wheat varieties within a species. As shown in Table 1, the average seed setting of Mindum × *A. elongatum* was 9.8%, while Pelissier × *A. elongatum* gave 36.9% success. It is apparent also that within *T. vulgare* there were wide variations in success, depending upon the variety used. In crosses involving *A. glaucum* similar differences in seed setting are also evident, although less striking. There are thus differences between varieties as well as between species groups in factors affecting compatibility.

The average crossing success with *A. glaucum* was found to be only about one-third of that of crosses involving *A. elongatum*. This is contrary to results of other investigators. Tzitzin (44) states that the two grass species "cross with equal success with nearly all species and forms of wheat". In crosses with species of *Triticum*, Armstrong (4) and Johnson (19) found that *A. glaucum* was at least equally as compatible as *A. elongatum*. To explain these differences the assumption can be made that different forms of the grass species were used by the different workers. Armstrong (4) has definitely shown that strains of *A. elongatum* give quite different crossing results. It is also possible that the same forms would react differently under different environmental conditions.

Working with material supplied by the writer, Thompson (50) found little or no difference in the percentage of ovules fertilized in crosses involving *A. elongatum* as compared to those involving *A. glaucum*. He found, however, that endosperm development was considerably more irregular in crosses involving the latter species. This difference in the ontogeny of the endosperm in these two groups of crosses undoubtedly accounts largely for the difference between them in seed setting. There was apparently nothing in Thompson's (50) results to support Johnson's (19) assumption of partial fertilization to account for "germless seeds".

Only a few crosses were attempted using grasses as the female parent. The results obtained from the crosses made in this direction are presented in Table 2.

Comparing Tables 1 and 2, it is seen that the percentage of seed setting was considerably lower when the grasses were used as female parents. Tzitzin (44) and Verushkine and Schechurdine (51) present similar data. On the basis of the success from numerous other inter-

TABLE 2.—RESULTS OF CROSSING *A. elongatum* AND *A. glaucum* AS FEMALE PARENTS WITH SPECIES AND VARIETIES OF *Triticum*

Male parent	Female parent—*A. elongatum*			Female parent—*A. glaucum.*		
	No. of florets pollinated	Percentage seed setting		No. of florets pollinated	Percentage seed setting	
		Av.	Max.		Av.	Max.
		%	%		%	%
T. dicoccum	30	0.00	—	—	—	—
T. durum—						
Mindum	57	5.26	8.7	—	—	—
Pelissier	135	5.18	13.3	—	—	—
T. polonicum	64	0.00	—	—	—	—
T. timopheevi	145	0.00	—	—	—	—
T. vulgare—						
Apex	70	0.00	—	—	—	—
Hope	18	0.00	—	—	—	—
Chinese	60	16.67	33.3	44	0	—
Marquis	—	—	—	150	0.67	3.84
Karkov	—	—	—	130	0	—
T. compactum—						
Little Club	505	4.21	16.7	—	—	—
Total and average	1084	2.95	—	324	0.31	—

specific and some other intergeneric reciprocal crosses (11, 27, 47, 64), the opposite result would be expected from *Triticum* × *Agropyron* reciprocal combinations, particularly in the case of those involving *A. elongatum.*

BACKCROSSING RESULTS

The F_1 hybrids were found to be highly or completely sterile and quite grass-like. In an effort to induce fertility and to lessen the dominancy of the grass characters, backcrossing to the wheat parent was practised.

It is generally known that in highly sterile hybrids the eggs are usually more viable than the pollen. Thompson (49) has pointed out that because of this fact the use of the F_1 as the female parent in backcrosses should give a much greater variety of progeny than the reciprocal, and greater possibilities in plant improvement. In view of this, the backcrosses in the present study were all made using the F_1 hybrids as females, although Tzitzin (44) had reported some success from the reciprocal combinations. The results of the backcrosses to the wheat parent are presented in Table 3.

Under open pollination the F_1 hybrids of the tetraploid wheats × *A. elongatum* and of both the tetraploid and hexaploid wheats × *A. glaucum* were almost completely sterile. As shown in Table 3, the backcrossing of the hybrids in these groups to their respective wheat parents resulted in practically no seed setting. On the other hand the hybrids of hexaploid wheats with *A. elongatum* were partially fertile under open pollination, and when backcrossed to the wheat parents an average seed setting of 4.5% was obtained. These results are in agreement with those of Veruskin (54) who found that when backcrossed to wheat the F_1 of *T. vulgare* × *A. elongatum* showed a tendency to fertility, while the F_1 of *T. durum* × *A. elongatum* were completely sterile.

It was feared that backcrossing to the wheats would result in an increase in annual forms and a reduction in winter hardiness. Consequently a limited amount of backcrossing was done to the grass parents. Keeping

TABLE 3.—CROSSING RESULTS WITH F_1 HYBRIDS BACKCROSSED TO WHEAT PARENTS

Wheat parent of F_1	Backcross male parent	Total no. of backcrossed			Percentage seed setting
		Plants	Florets	Seeds	
Hybrids of tetraploid wheats with *A. elongatum*					
					%
Vernal	Vernal	12	540	0	0.0
Mindum	Mindum	3	120	1	0.8
Pelissier	Pelissier	18	1812	0	0.0
Polish	Polish	8	280	0	0.0
T. timopheevi	*T. timopheevi*	5	546	1	0.18
Total and average		46	3298	2	0.06
Hybrids of hexaploid wheats with *A. elongatum*					
Hope	Hope	8	138	6	4.3
Apex	Apex	8	334	16	4.8
Marquis	Marquis	31	1019	47	4.6
Marquis	Apex	1	27	3	11.1
Little Club	Little Club	6	234	8	3.4
Total and average		54	1752	80	4.57
Hybrids of wheats with *A. glaucum*					
Mindum	Mindum	3	60	0	0.0
Pelissier	Pelissier	2	60	0	0.0
Marquis	Marquis	1	40	0	0.0
Total and average		6	160	0	0.0
Grand total and average		106	5210	82	1.58

TABLE 4.—RELATIONSHIP BETWEEN FERTILITY OF F_1 HYBRIDS WHEN OPEN POLLINATED AND WHEN BACKCROSSED

F_1 hybrid of	Partially fertile when open pollinated		Sterile when open pollinated	
	No. of plants	Plants partially fertile backcrossed	No. of plants	Plants partially fertile backcrossed
Backcrossed to wheat parent				
		%		%
Tetraploid wheats × *A. elongatum*	—	—	46	4.35
Hexaploid wheats × *A. elongatum*	19	68.42	17	17.65
Triticum spp. × *A. glaucum*	—	—	6	0.0
Total and average	19	68.42	69	7.25
Backcrossed to grass parent				
Tetraploid wheats × *A. glaucum*	—	—	16	6.25
Hexaploid wheats × *A. elongatum*	14	28.57	21	4.76
Total and average	14	28.57	37	5.40

the objective of the project in mind, this latter procedure was also theoretically objectionable on account of the resultant concentration of genes for small seed size. Of the 1599 florets on 36 F_1 plants of *A. elongatum* parentage and 16 F_1 plants of *A. glaucum* parentage backcrossed to the grass parent, only 0.5% of the florets set seed. Backcrossing to the grass parent was thus less successful than backcrossing to the wheat parent.

The relationship between fertility of the F_1 hybrids under open pollination and when backcrossed is more clearly shown in Table 4.

A fairly high percentage of plants which were fertile under open pollination were also fertile when backcrossed, particularly when backcrossed to the wheat parent. However, of the group which were sterile when open pollinated, only a small percentage of plants set seed when backcrossed, and the percentage of florets setting seed was very low. Although the occasional plant which was sterile under open pollination was partially fertile when backcrossed, this procedure was obviously not a very practical means of inducing fertility in material which was highly sterile under open pollination conditions. This is clearly emphasized by the fact that in the F_1 hybrids of tetraploid wheats $\times$ *A. elongatum*, and of *Triticum* species $\times$ *A. glaucum*, a total of 68 plants and 3857 florets were backcrossed to one or other parent, and only 3 seeds were obtained.

CHARACTERISTICS OF PROGENIES OF *A. ELONGATUM* PARENTAGE

Vigour

Unusual vigour of growth is of very general occurrence in F_1 hybrids, and the first generation of *Triticum* spp. by *A. elongatum* was no exception to this general condition. The *Triticum-Agropyron* plants of the F_1 generation were, as a rule, slightly shorter growing than the plants of the grass parent, but considerably taller growing than the plants of the wheat parents. The F_1 closely resembled the grass parent in the degree of stooling. Johnson (19) and Wakar (60) have noted that the F_1 displayed hybrid vigour.

The plants of the F_2 and later generations were considerably less vigorous than the F_1. They were shorter growing and markedly less strongly stooling, particularly in their first year of growth. Only the occasional plant was observed to be as vigorous as the average of the F_1. There was no noticeable decrease in average vigour with advancing generations, but there was evidence of decreasing variability. By F_4 certain lines were surprisingly uniform with respect to vigour.

In height and stooling the backcross generations were very similar to that of the F_2, but were less variable.

Growth Habit

The type of growth in the year of planting is a character in which plants of the spring wheats differed from plants of *A. elongatum* and the winter wheats. A very large percentage of the plants of the grass parent failed to head during their first year of growth. The data on the habit of growth in the year of seeding the F_1 to F_4 hybrids of spring and winter wheats $\times$ *A. elongatum* are given in Table 5.

In the F_1 generation derived from spring wheats crossed with *A. elongatum*, the spring habit of growth of the wheat was found to be almost completely dominant to the winter habit of the grass. It has been shown that the spring habit is dominant in the intervarietal wheat crosses (14, 15, 37). Tzitzin (44) noted that the F_1 of the crosses of spring wheats with species of *Agropyron* tended to head the first year, while those from winter wheats failed to head. Lapin (26) and Cicin (9) report similar observations.

With the exception of the population from Little Club, the F_2 of spring wheat parentage showed around 5% winter forms, while the F_2 of winter wheat lineage produced about 90% winter forms. No explanation can be offered for the greater proportion of winter forms in the F_2 population of the Little Club hybrids. The low average percentage of winter forms in the F_3 and F_4 generations should not be interpreted to mean that those generations were becoming pure breeding for the spring habit, as these generations were grown from seed harvested from F_2 or F_3 plants in their first year of growth, and thus displaying the spring habit of growth.

TABLE 5.—SPRING VERSUS WINTER HABIT IN F_1 TO F_4 GENERATIONS OF HEXAPLOID WHEAT × *A. elongatum*

Female parent	F_1		F_2		F_3		F_4	
	No. of plants	Percentage winter habit	No. of plants	Percentage winter habit	No. of plants	Percentage winter habit	No. of plants	Percentage winter habit
Spring wheats × *A. elongatum*								
		%		%		%		%
Apex	30	0 0	540	5.56	380	6.05	341	1.47
Marquis	72	0.0	95	5.26	422	0.0	378	0 00
Chinese	45	2.22	20	0.00	—	—	—	—
Little Club	121	4.13	80	25.00	316	1.89	—	—
Total and average	268	2.24	735	7.48	1119	2.59	719	0.70
Winter wheats × *A. elongatum*								
Karkov	47	100.0	99	86.87				
Dawson	—	—	38	97.37				
Total and average	47	100.0	137	89.78				

Several Russian investigators (8, 9, 44, 52, 53) have reported the proportion of perennial and annual plants in the various generations of *Triticum-Agropyron* hybrids, but they have not stated how these two life habits were distinguished. Plants which winter kill may do so because they are annuals or because they are perennials which lack winter hardiness. In other words, winter survival records do not distinguish between the annuals and the non-hardy perennials. It is necessary, therefore, to attempt to distinguish the annuals and perennials by the appearance of the plants late in the fall of the year of seeding.

The F_1 plants which headed in the year of seeding almost invariably displayed an indeterminate type of growth. It was assumed that this was an expression of the perennial habit. Contrasted to the indeterminate type of growth in the F_1 generation, it was observed in the F_2 and later generations that some plants appeared which in their first year of growth

displayed a tendency to "ripen off". On these plants the heads, culms and leaves turned a straw colour in the fall before damaging frosts occurred. This characteristic was very clear cut in some plants, while there was a more or less intermediate condition in others. A record was taken of each plant which showed a tendency to "ripen off", and the data in this connection are summarized in Table 6. While it is unlikely that this phenomenon provides a completely accurate criterion for separating annual from perennial forms, it probably does give some indication of the proportion of annuals.

TABLE 6.—FREQUENCY OF OCCURRENCE OF "RIPENING OFF" IN VARIOUS GENERATIONS OF HYBRIDS OF *A. elongatum* PARENTAGE

Wheat parent	F_1		F_2		F_3		F_4		2nd generation after backcrossing F_1*		3rd generation after backcrossing F_1*	
	No. of plants	Percentage ripened off	No. of plants	Percentage ripened off	No. of plants	Percentage ripened off	No. of plants	Percentage ripened off	No. of plants	Percentage ripened off	No. of plants	Percentage ripened off
		%		%		%		%		%		%
Apex	24	0.0	675	4.15	578	11.07	341	4.69	3	33.33	19	21.05
Marquis	50	0.0	336	0.00	832	0.36	378	1.59	14	14.28	77	5.19
Chinese	32	0.0	51	0.00	—	—	—	—	—	—	—	—
Hope	10	0.0	17	23.50	—	—	—	—	90	2.22	206	15.53
Karkov	31	0.0	103	0 97	—	—	—	—	—	—	—	—
Little Club	71	0.0	204	1.96	317	0.63	—	—	4	0.0	—	—
Total and average	218	0.0	1386	2.67	1727	4.00	719	3.06	111	4.50	302	13.24

* Backcrosses of F_1 to wheat parents.

Assuming that "ripening off" gives an index of the annual habit, it is seen from Table 6 that the F_1 are all perennial which is in agreement with the results of several other investigators (4, 5, 9, 19, 44, 52). As an average 2.6% of the F_2, 4.0% of the F_3 and 3.0% of the F_4 are "annuals". No explanation can be offered, however, for the failure to find this habit of growth in the F_2 of Marquis and Chinese parentage or for its frequent occurrence in the segregating generations of Apex lineage. Considering only the average frequency of occurrence of "ripening off", it is evident that there is a comparatively small percentage of recovery of the "ripening off" characteristic of wheat in the F_2 to F_4 generations.

If the assumption that "ripening off" is an index of annual habit is not accepted, at least it can be definitely said that it is a character inherited from the wheat parents. The data in Table 6 show that the frequency of occurrence of the character is increased by backcrossing to the wheat.

Winter Hardiness

Winter hardiness is a character of paramount importance in perennial forage crops for northern latitudes. In the attempt to develop a perennial grass from hybrids of *Triticum* × *Agropyron* the hardiness character of the grass must be retained if the objective is to be attained.

The results on the winter survival of the F_1 generation are given by years in Table 7. With the exception of one year (1936–37), and as an average of all years, the crosses of tetraploid wheat parentage showed a

higher percentage survival than did the crosses of hexaploid wheat lineage. The explanation of this phenomenon may lie in the fact that in the hybrids derived from tetraploid wheats 28.5% of the chromosomes are from wheat, while in the hybrids derived from hexaploid wheats 37.5% of the chromosomes are from wheat. The wheat chromosomes bring in genes for annual habit and lack of hardiness, and it is logical to expect that the higher the proportion of those chromosomes the lower will be the winter hardiness.

It was expected that the F_1 progenies from winter wheat × *A. elongatum* would show greater hardiness than those of spring wheat parentage, but there was no evidence of this to be found in the data on the F_1 hybrids. Certain varietal differences did, however, appear. Mindum and Chinese produced hybrids which were quite consistently low in percentage survival, and the surviving plants were injured to a greater extent than those of other varieties within their respective chromosome groups. The reason for this varietal difference is unknown, but it indicates that some spring wheats carry different genes for hardiness than others.

The results on winter survival of F_2 to F_4 and 1st to 3rd generation

TABLE 7.—WINTER SURVIVAL OF F_1 HYBRIDS OF SPECIES AND VARIETIES OF *Triticum* × *A. elongatum*

Female parent	Winter '36–37		Winter '37–38		Winter '38–39		Average percentage surviving
	No. of plants	Percentage surviving	No. of plants	Percentage surviving	No. of plants	Percentage surviving	
Diploid wheats × *A. elongatum*							
Haynaldia villosa	—	% —	—	% —	4	% 0 0	% —
Tetraploid wheats × *A. elongatum*							
T. dicoccoides	—	—	9	66.7	7	100 0	81.3
T. dicoccum	170	84.7	27.8	95 3	265	98.9	94.1
T. durum—							
Mindum	29	51 7	31	74.2	25	56 0	61.2
Pelissier	60	68.3	285	84.9	246	90.6	85 6
T. turgidum	—	—	26	92.3	24	95.8	94 0
T. polonicum	36	83.3	46	84.8	34	85.3	84 5
T. timopheevi	—	—	37	94.6	35	97.1	95.8
T. pyramidale	—	—	—	—	12	66.7	—
Total and average	295	77.97	712	89.04	648	92.60	88 46
Hexaploid wheats × *A. elongatum*							
T. vulgare—							
Apex	9	77.8	25	88.0	24	87.5	86.2
Marquis	30	90.0	74	67.6	50	92.0	79.9
Chinese	—	—	42	57.1	32	25.0	43.2
Hope	4	100.0	9	55.6	10	80.0	73.9
Karkov	46	78.3	43	72.1	31	93.6	80.0
Dawson	—	—	—	—	12	83.3	—
Minhardi	—	—	—	—	6	100.0	—
T. compactum	—	—	139	51.1	71	90.1	64 3
Total and average	89	83.15	332	61.02	236	81.36	71.39
Grand totals and average	384	79.17	1044	80.17	888	89.19	83 46

after backcrossing the F_1 to wheat are summarized in Table 8. The data represent the average survival for the winters 1938–39 and 1939–40, and pertain to the survival the first winter after the plants were set out except in the case of progenies of Karkov parentage. Since the winter habit of growth in the year of seeding progenies of Karkov × *A. elongatum* was found to influence survival, the data for this cross give the survival the winter after the second year of growth in the field.

TABLE 8.—WINTER SURVIVAL OF F_2 TO F_4 OF NON-BACKCROSSED GENERATIONS (WHEAT × *A. elongatum*) AND OF 1ST TO 3RD GENERATIONS AFTER BACKCROSSING F_1 TO WHEAT PARENT (WHEAT × *A. elongatum* × WHEAT). NUMBER OF PLANTS AND AVERAGE SURVIVAL FOR WINTERS 1938–39 AND 1939–40

Wheat parent	Non-backcrossed generations						Backcrossed generations					
	No. of plants			Percentage survival			No. of plants			Percentage survival		
	F_2	F_3	F_4	F_2	F_3	F_4	1st	2nd	3rd	1st	2nd	3rd
				%	%	%				%	%	%
Apex	672	554	332	28.7	18.6	6.0	1	8	19	0.0	12.5	10.5
Marquis	338	828	379	50.6	19.8	9.2	6	35	77	16.7	8.5	0.0
Hope	14	31	—	21.4	0.0	—	1	89	193	0.0	1.1	0.0
Karkov	12	—	—	16.6	—	—	—	—	—	—	—	—
Little Club	200	317	—	36.0	3.1	—	—	12	—	—	16.7	—
Total and average	1236	1730	711	35.68	16.01	7.74	8	144	289	12 50	4.96	0.69

The average winter survival of all F_2 hybrids of hexaploid wheats × *A. elongatum* was found to be 35.6%. The average survival of the F_1 of this group of crosses was shown in Table 7 to be 71.3%. On the average therefore, there was a reduction of approximately 50% in the survival of the F_2 as compared to the F_1. A significant drop in percentage survival from F_1 to F_2 occurred consistently in all crosses. The differences in survival which appear between the F_2 of various crosses are probably due to chance fluctuations, and do not represent true differences in hardiness. It is interesting to note that the F_2 plants derived from the winter variety Karkov were probably less hardy than the F_2 of spring wheat parentage. It was noted earlier that the F_1 of winter wheat parentage were no hardier than those of spring wheat parentage.

Comparing the F_2 with the F_3 and F_4, it is seen from Table 8 that the survival of plants of each succeeding generation was at least 50% lower than that of the previous one. A drop of at least that magnitude occurred consistently in each cross.

It is evident that following backcrossing to the wheat parents, the survival is significantly lower than in comparable non-backcrossed material. The survival of the backcross material displays a trend to decrease markedly with each succeeding generation, being similar in this respect to the F_2 to F_4. While backcrossing to wheat decreases hardiness, backcrossing to *A. elongatum* increases hardiness, as evidenced by the fact that 6 plants of the 1st generation backcross of the F_1 to the grass were in the field the winter of 1939–40. and all plants survived with practically no injury.

It has been stated above that in hybrids of Karkov × *A. elongatum* the winter habit of growth in the year of seeding influenced the survival the first winter in the field. This is shown by the fact that 100% of the 12 F_2 plants of the above cross survived the first winter, but in the second winter only 16.7% of the plants survived. Tzitzin (44) has reported that the hybrids of *Agropyron* sp. by winter wheats were more hardy than those by spring wheats, but in making this observation he may not have taken into account the influence which habit of growth had on the results.

Several investigators have made observations on the winter survival of the advanced generations of hybrids of *A. elongatum* parentage. Armstrong et al. (5) reported that at Ottawa, Canada, the F_2 survived between 94.7% and 97.2%, and the 2nd generation backcross between 26.6% and 27.4%. Tzitzin (44) found the percentage of perennial (winter hardy) plants to be 73.2% in F_2, 30.7% in F_3, and 1% in F_4, but stated that some F_3 lines were 80% perennial. Veruskine (52) reported that the perennial habit was dominant in the F_1 but that the proportion of perennials fell to between 40 and 70% in F_2, 5% in F_3, and only occasional plants were perennial in F_4 and none in F_5 to F_7. Veruskine (53) later reported that over 90% of the F_2 and F_3 were perennial. Cicin (9) recorded a similar drop in survival from F_1 to F_2, but stated that in F_4 the perennial forms constituted from 0 to 60 or 70% of the population, depending upon the line. He stated that in F_5 it was possible to select valuable annual or perennial forms. Elsewhere Cicin (8) stated that constant annual or perennial forms could be selected as early as F_3. In 1936 it was reported (3) that Tzitzin had two perennial types in large increase fields. Although differing in detail, the writer's data display the same general trends as shown by the results of several of the investigators cited above.

A comparison of the winter survival of F_3 progenies derived from different F_2 plants is given in Table 9. The data are taken from the Melfort nursery only, since it was found that variations in vigour in the fall influenced the winter killing at Saskatoon. It should be pointed out that the seed which gave rise to these F_3 plants was in all cases harvested from F_2 plants in their first year of growth, and consequently none of the non-hardy F_2 plants had been eliminated.

It is clearly seen that certain F_3 families showed a much higher percentage survival than did others. In other words some F_2 plants were genetically fairly winter hardy, while other F_2 plants lacked factors for hardiness. Further evidence of this fact was obtained by comparing the winter survival of the same F_3 families in the two nurseries. Although the data from the Saskatoon nursery was affected by variation in plant vigour, it was found that those F_3 families ranking highest for survival at Melfort were also in the highest survival groups at Saskatoon, and that there was a similar relationship in the lowest survival groups. The wide range of percentage survival indicates that a large number of factors were operating. It is interesting to note that complete killing occurred in only one of the 16 F_3 families, and thus with respect to survival factor only one of the 16 F_2 plants was of a genetic constitution similar or approaching that of the wheat parent.

TABLE 9.—SURVIVAL OF DIFFERENT F_3 FAMILIES, WINTER 1938–39 (MELFORT)

Wheat parent—Apex				Wheat parent—Marquis			
Family number	No. of plants	Percentage survival	Survival score of F_2 parent	Family number	No. of plants	Percentage survival	Survival score of F_2 parent
		%				%	
3–111	20	75.00	1	1–26	9	66.67	2
3–16	11	72.73	0	1–153	16	62.50	1
6–93	16	68.75	1	1–110	9	44.40	0
3–51	12	66.67	0	1–169	9	33.33	–
6–10	6	33.33	2	1–159	6	33.33	0
3–29	6	16.67	0	1–152	16	31.25	0
				1–188	7	28.57	0
				1–146	41	24.39	0
				1–68	11	9.09	0
				1–11	8	0.00	0

TABLE 10.—SEED SETTING OF F_1 HYBRIDS OF SPECIES AND VARIETIES OF *Triticum* × *A. elongatum*

Female parent	Total no. of plants harvested	Ave. percentage of harvested plants fertile	Ave. percentage of florets setting seed	Maximum fertility observed
Diploid wheat derivatives				
H. villosa	4	% 0.0	% 0.0	% —
Tetraploid wheat derivatives				
T. dicoccoides	11	18.2	0.08	0.26
T. dicoccum	193	1.0	0.03	0.54
T. durum—				
Mindum	47	0.0	0.0	—
Pelissier	86	0.0	0.0	—
T. turgidum	38	7.9	0.01	0.71
T. polonicum	55	1.8	0.01	0.16
T. timopheevi	47	12.8	0.04	1.54
T. pyramidale	4	—	—	—
Total and average	481	2.9	0.02	—
Hexaploid wheat derivatives				
T. vulgare—				
Apex	68	44.1	2.75	28.37
Marquis	162	27.2	1.56	29.25
Chinese	71	38.0	0.31	5.34
Hope	18	16.7	0.41	6.94
Karkov	40	32.5	0.33	5.17
Lutescens	5	—	—	—
Dawson	4	—	—	5.95
Minhardi	6	—	—	—
T. compactum	179	31.3	0.31	6.33
Total and average	553	32.0	0.94	
Grand total and average	1034	18.5	0.67	

Fertility

Fertility was determined on a floret basis. A count of the total number of spikelets on from 3 to 5 heads multiplied by the average number of florets per spikelet gave a quick calculation of the total number of florets. The determination of the number of seeds from the 3 to 5 heads then provided a measure of fertility. The highly significant r value of $+0.78$ between the 1938 and 1939 fertility of the same 259 F_1 plants is evidence of the reliability of the method. The data on the fertility of F_1 plants of *A. elongatum* parentage are summarized in Table 10.

As shown by Table 10, the small population of F_1 plants derived from diploid wheat crosses was completely sterile. In the case of the F_1 of tetraploid wheat parentage only 2.9% of the plants and only 0.02% of the florets set seed. This latter group of hybrids were thus almost completely sterile. The derivatives of hexaploid wheat were moderately fertile, an average of 32.0% of the plants and 0.9% of the florets set seed, and the maximum fertility observed was considerably higher than in the case of the tetraploid wheat derivatives. In general the seed setting results reported by other workers are confirmed by the present study.

Tzitzin (44) noted that F_1 plants were generally self-sterile but that 60 F_1 plants of *T. vulgare* × *A. elongatum* had a low degree of fertility. Later Tzitzin (46) reported that the highest seed setting was found in an F_1 plant of *T. durum* × *A. elongatum*. Veruskin (52) reported that as a rule F_1 plants were sterile but that some fertile plants were found, particularly in crosses of the soft wheats with *A. elongatum*. Lapin (26) found some *Triticum* × *A. elongatum* F_1 plants which were fertile. Cicin (9) stated that only individual groups of F_1 were self-fertile, the majority being self-sterile. Hiznjak (17) recorded that the F_1 plants of tetraploid wheats × *A. elongatum* were sterile, and some of those of hexaploid wheats × *A. elongatum* were fertile. Armstrong (4) observed that, with the exception of one plant, the F_1 were sterile when grown in the greenhouse. Johnson (19) confirmed the results obtained by Armstrong in the greenhouse, and showed that in the field the F_1 of hexaploid wheat × *A. elongatum* was fairly fertile, while the F_1 of tetraploid wheats × *A. elongatum* were completely sterile one year but set seed fairly well the next year. In the F_1 of *T. vulgare* × *A. elongatum* Peto (35) found that the self-fertile plants had less than 7 bivalents, while self-sterile plants had 14 or more univalents. Wakar (59) recorded that F_1 plants of *T. durum* × *A. elongatum* which had 21 bivalents plus 7 univalents were fertile, whereas the plants which had only 14 bivalents were sterile.

A close correspondence between the average proportion of good pollen and the average fertility was found. In the F_1 of tetraploid wheats × *A. elongatum* 4.0% of 3909 pollen grains examined from 50 plants were good, while from the F_1 of hexaploid wheat derivation 30.4% of 8339 pollen grains examined from 107 plants were good. No correlation between these two phenomena could be demonstrated on a single plant basis. Johnson (19) concluded that there was a "direct correlation between the proportions of good pollen and seed-set when the proportions are sufficent to give anther dehiscence". Armstrong et al. (5) found a similar relationship.

The leathery nature of the anthers and the failure of these to dehisce have been observed by Tzitzin (44), Armstrong (4), Johnson (19). Differences between plants have been observed. Tzitzin (44) found that the 60 fertile F_1 plants of *T. vulgare* × *A. elongatum* referred to above had normal anther dehiscence. Johnson (19) and Armstrong et al. (5) reported a correlation between dehiscence and the ratio of good to bad pollen. Both authors considered that when there was a relatively large proportion of good pollen grains, sufficient internal pressure was eventually exerted to give dehiscence, but when pollen development was poor, insufficient pressure was exerted to bring about dehiscence.

The data concerning the fertility of the F_2 to F_4 are summarized in Table 11. From this table it is seen that there is a definite trend for fertility to increase with each advance in generation. This is displayed both in the percentage of plants and the percentage of florets which were fertile. The increase in fertility is particularly pronounced from F_1 to F_2 (cf. Tables 10 and 11) and from F_2 to F_3, but is less marked from F_3 to F_4. The trend is further shown by Figure 1 which presents diagrammatically the frequency distribution for percentage fertility in F_1 to F_4 generations.

TABLE 11.—SEED SETTING OF F_2 TO F_4 GENERATIONS OF SPECIES AND VARIETIES OF *Triticum* × *A. elongatum*

Wheat parent	Total no. of plants harvested			Average percentage of fertile plants			Average percentage of fertile florets		
	F_2	F_3	F_4	F_2	F_3	F_4	F_2	F_3	F_4
Tetraploid wheat derivatives									
				%	%	%	%	%	%
T. polonicum	4			75.0			9.13		
T. timopheevi	4			0.0			0.0		
Total and average	8			37.5			5.64		
Hexaploid wheat derivatives									
Apex	486	453	182	45.9	55.8	72.0	3.60	7.36	10.59
Marquis	452	540	189	43.6	70.9	71.4	4.22	9.47	9.03
Chinese	40			47.5			4.73		
Hope	4			75.0			5.01		
Karkov	24			41.7			1.13		
Dawson	1			0.0			0.0		
Little Club	125	216		32.8	86.1		2.91	9.27	
Total and average	1132	1109	371	43.6	69.1	71.7	3.70	8.83	9.75

From Figure 1 it is seen that the percentage of the population falling in the lowest fertility group decreased with each advancing generation, and conversely the proportion of the population in the higher fertility groups increased from F_1 to F_4 progressively. Veruskin (53), Tzitzin (44), Johnson et al. (20), and Armstrong et al. (5) have all observed that fertility increased as the generations advanced.

The fertility data for the 1st to 3rd generations after backcrossing the F_1 to the wheat parents are given in Table 12.

It is seen from Table 12 that in the 1st generation after backcrossing the F_1 to the wheat parent the average fertility is lower than that of the

TABLE 12.—SEED SETTING OF 1ST TO 3RD GENERATIONS AFTER BACKCROSSING THE F_1 OF *Triticum* SP. × *A. elongatum* TO WHEAT

Wheat parent	Total no. of plants harvested			Ave. percentage of fertile plants			Ave. percentage of fertile florets		
	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
Apex	4	7	19	75.0	57.1	78.9	3.60	9.52	5.84
Marquis	18	17	72	33.3	82.4	66.7	1.41	8.74	7.91
Chinese	1	—	—	0.0	—	—	0.00	—	—
Hope	5	95	186	40.0	82.1	89.8	8.39	16.26	29.72
Little Club	9	4	—	11.1	100.0	—	0.21	18.79	—
Total and average	37	123	277	26.9	81.3	83.0	1.76	14.57	20.86

F_2 generation of the same crosses as given in Table 11. However, the hybrids of Hope parentage displayed exceptionally high fertility. Exceptionally high fertility was again displayed by the progeny of Hope parentage in the 2nd and 3rd generation after backcrossing. The fertility of Little

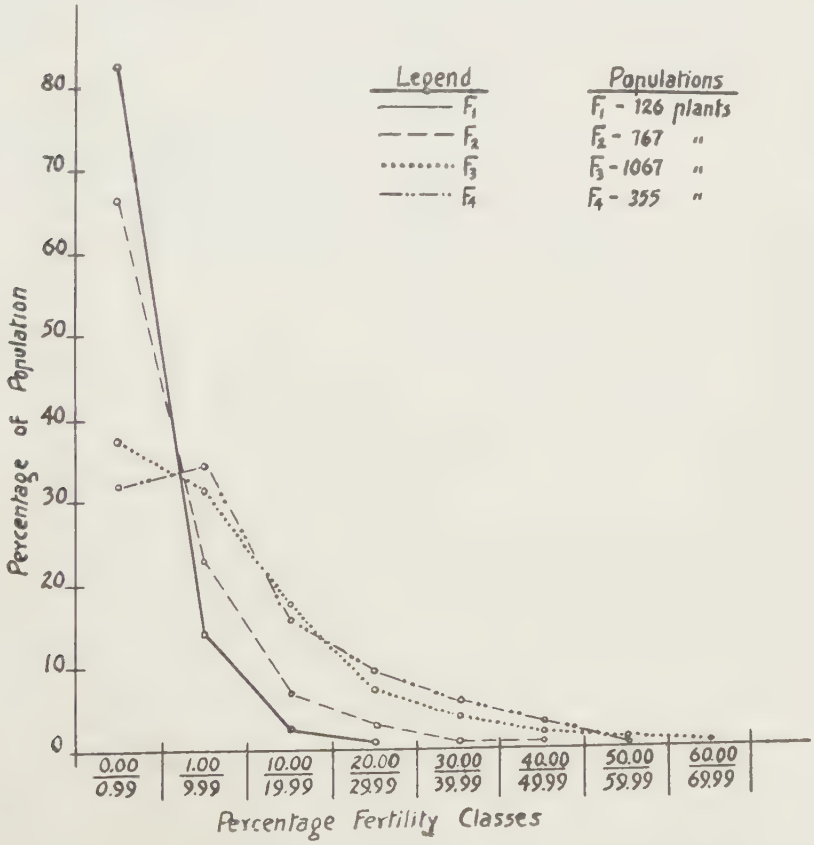

FIGURE 1. Graph of frequency distribution for percentage fertility in F_1 to F_4 of Hexaploid wheats × *A. elongatum.*

Club derivatives in the 2nd generation after backcrossing was likewise high, being double that of the open pollinated F_3 population of Little Club parentage, (cf. Table 11). No such marked increase in fertility was found in the 2nd and 3rd backcross generations of Apex and Marquis parentage, the fertility of which was quite similar to that of the ordinary F_3 and F_4 populations of these wheat parents.

The outstandingly high fertility of the 3rd generation backcross of Hope parentage is further emphasized when a comparison is made with the fertility of wheat. Computed in the same way as was done in the case of hybrid material, the fertility of Marquis wheat in 1939 was found to be around 65%. While the fertility of the Hope variety was not ascertained, it is likely that it would be quite similar to that of Marquis. Table 12 shows that the average fertility of 186 3rd generation backcross plants derived from Hope was 29.7%, which is only slightly less than one-half the fertility of the wheat parent.

The parents of the F_3 and F_4 progenies set out in 1939 were selected as far as possible for high fertility. The correlation between the fertility of the parents and the average fertility of their progenies was found to be $+0.22$ ($n = 50$), which was lower than the 5% level of significance. It was thus impossible to demonstrate that selection had had a significant effect upon the fertility of the progenies.

Seed Characters

The primary breeding objective of the present study was to obtain the large seed size of *Triticum* sp. in a perennial grass. As compared to existing species of *Agropyron*, the improvement in seed weight which might be attained in a *Triticum* × *Agropyron* hybrid is indicated by the fact that seed of *A. elongatum*, with lemma and palea attached, weighs less than one-quarter of that of the naked seed of *T. vulgare*, and seed of *A. elongatum*, weighing on the average 6.89 grams per thousand kernels, is larger than that of most species of that genera.

Throughout the present study seed weight has been used as a measure of seed size. The seed was weighed on an analytical balance which was read to the nearest third decimal gram. In order to avoid the use of cumbersome decimals, the weights were converted to a thousand seed basis.

Although exhibiting considerable variation, the F_0 seed from the tetraploid wheats was found to weigh about 50% higher than the F_0 seed from hexaploid wheat parents. But expressed as a percentage of the weight of the seed of the wheat parents, the F_0 seed derived from tetraploid wheat species averaged 65.3%, while those derived from hexaploid wheat parentage averaged 65.4%. Armstrong (4), on the contrary, reports that F_0 seed of tetraploid wheats × *A. elongatum* was about one-third the weight of seed of the wheat parent, while hexaploid wheats gave hybrid seeds about one-third to one-half the weight of the wheat parent. Tzitzin (44) also found that the hybrid seed weight of *T. durum* × *A. elongatum* was less than that of *T. vulgare* × *A. elongatum*.

In spite of abnormal endosperm development, the germination of F_0 seed was remarkably high. The average germination of all F_0 seed was 80.1%. The hybrid seed obtained from the hexaploid wheat parents

germinated considerably higher than that secured from the tetraploid or diploid wheats, a fact which cannot be explained on the basis of seed weight. Tzitzin (44) observed a similar difference in the case of *T. durum* × *Agropyron* species as compared to *T. vulgare* × *Agropyron* species, and attributed the lower germinating capacity of the seed of the former hybrids to poor embryo development.

The data on the weight of the seed obtained from plants of F_1 to F_4 and backcross generations are summarized in Table 13 in the form of a frequency distribution. The table shows that with each advancing generation there was a marked trend for the seed weight to drop, a trend which was also noted by Armstrong et al (5). In general, by F_3 and F_4 the average seed weight was very little greater than in the grass parent, and no plants with exceptionally high seed weight were found, although Tzitzin (44) reported finding some F_3 plants having a thousand kernel weight of 30 grams. In contrast to the F_1 to F_4, the backcross progenies displayed no indication of a trend for seed weight to decline with advancing generations.

Exceptionally high seed weights were found in some plants of the back cross progenies of Little Club and Hope parentage. A few plants were obtained in the populations of these hybrids having a seed weight of over 20 grams per thousand kernels. The maximum observed was 22.3 grams in a second generation backcross plant of Little Club parentage. The kernels in these plants were quite similar in size to those of the *T. vulgare* varieties of wheat. Thus the backcross material in general, and that of the crosses noted above in particular, are much more promising with respect to seed size than the non-backcrossed material.

From the foregoing data it is clearly evident that rigid selection for

TABLE 13.—FREQUENCY DISTRIBUTION FOR SEED WEIGHT OF PLANTS OF F_1 TO F_4 AND BACKCROSS GENERATIONS

Parent or generation of hybrid	No. of plants	Percentage of plants with seed weight of								
		1.0 4.2	*4.3* 8.4	*8.5* 12.6	*12.7* 16.8	*16.9* 21.0	*21.1* 25.2	*25.3* 29.4	*29.5* 33.6	*33.7* 37.8
Parental material										
		%	%	%	%	%	%	%	%	%
A. elongatum	5		100.0							
Apex	12							25.0	33.3	41.7
Marquis	28					3.6	14.3	64.3	10.7	
Little Club	3					33.3	66.7			
Hope	13							15.4	23.1	61.5
F_1 to F_4 generations										
Combined F_1	121	3.3	19.0	48.8	26.4	2.5				
Combined F_2	479	39.9	32.8	21.3	5.8	0.2				
Combined F_3	804	52.7	34.2	11.7	1.4					
Combined F_4	274	71.9	26.3	1.5	0.4					
Generations after backcrossing F_1 to wheat parent										
Combined 1st	12	—	8.3	33.1	41.7	16.7				
Combined 2nd	102	4.9	24.5	37.3	26.5	5.9	1.0			
Combined 3rd	229	9.6	24.9	35.8	21.8	7.4	0.4			

high seed weight will be necessary. That selection in this character is at least partially effective was demonstrated by correlating the seed weight of 49 parent plants with the average seed weight of their progenies. The correlation was found to be +0.39, a highly significant value.

Germination of the seed from F_1 to F_3 plants was surprisingly good in view of the poor seed development. The average germination for seed from F_1, F_2, and F_3 plants was 70.8, 76.9, and 65.3% respectively. The plumper seed from the backcrosses to wheat had a higher germination than the non-backcrossed material.

The caryopsis of *A. elongatum* is tightly enclosed within the lemma and palea, and in this respect the grass differs from the hexaploid wheats which have naked seed. The hybrid seeds were studied for this characteristic, although as a result of the method of threshing some difficulty was experienced in making accurate comparisons.

Among the seed from F_1 plants of hexaploid wheat × *A. elongatum* the expression of seed coat adherence was found to vary over a wide range. However, the modal class was wheat-like or near wheat-like, which indicates a partial dominance of the naked character inherited from the wheat parent. In the F_2 of all crosses there was a substantial increase in the proportion of plants with naked or nearly naked seeds. The distribution in the F_3 varied considerably depending upon the cross, but in general the seed from this generation was similar to that from F_2 plants. The F_4

TABLE 14—FREQUENCY DISTRIBUTION FOR GLUME WIDTH (CMS.) OF PARENTS AND HYBRID GENERATIONS

Parent or wheat parent of hybrid	Generation	No. of plants examined	Percentage of plants in glume width class							
			0.13–0.16	0.17–0.20	0.21–0.24	0.25–0.28	0.29–0.32	0.33–0.36	0.37–0.40	0.41–0.44
			%	%	%	%	%	%	%	%
A. elongatum	Parental	61	26.2	68.9	4.9					
Apex	Parental	20						10.0	65.0	25.0
Apex	F_1	57		7.0	22.8	61.4	8.8			
	F_2	347	0.3	5.8	35.7	32.6	25.4	0.3		
	F_3	287	0.7	5.6	23.3	34.8	30.7	3.8	1.0	
	F_4	151		7.3	27.2	37.1	27.8			0.7
Marquis	Parental	48						2.1	72.9	25.0
Marquis	F_1	107		6.5	42.1	44.9	6.5			
	F_2	449	0.4	5.8	29.2	42.1	17.6	4.7	0.2	
	F_3	450	0.2	1.6	10.7	43.1	31.8	10.0	2.7	
	F_4	189		1.1	10.1	41.3	41.3	5.8	0.5	
Backcrosses of F_1 to wheat parents										
Apex	1st*	4				50.0	25.0	25.0		
	2nd	4				50.0	50.0			
Marquis	1st	18			22.2	27.8	38.9	11.1		
	2nd	7			14.3	28.6	42.9	14.3		

* After the backcross.

displayed a decided increase in the proportion of plants with naked seeds. In all generations fairly typical grass types were found in only 3 plants which were all derived from Little Club.

The evidence from the F_1 generation that the naked seed character of wheat is at least partially dominant is further supported by the data from the 1st backcross generation. The seed from 1st generation backcross plants of Apex, Marquis, and Hope parentage were very largely wheat-like with respect to seed coat adherence. The small population derived from Little Club tended to be of an intermediate condition.

Contrary to the results given above, Armstrong et al. (5) found that there was a definite tendency for the F_2 population to resemble the grass parent with respect to seed coat adherence.

Seedling, Stem, Leaf, and Head Characters

By means of frequency distributions the characteristics of the hybrids were compared with those of the parents for each of the following characters: primary root number, primary leaf vein number, leaf texture, stem hollowness, spike density, glume width, beak type, awning, and number of florets per spikelet. Table 14 presents a frequency distribution for glume width of the parents and the hybrid generations of some crosses. It illustrates the manner in which each character was studied.

Table 15 summarizes the character expressions of the F_1 material of all crosses involving *A. elongatum*.

TABLE 15.—EXPRESSION OF SEEDLING, STEM, LEAF, AND HEAD CHARACTERS IN F_1 HYBRIDS OF *Triticum* SP. × *A. elongatum*

Characters displaying dominance of grass type	Characters displaying partial dominance of grass type	Characters displaying dominance of wheat type
Awning. Glume width.	Primary root number. Primary leaf vein number. Leaf texture. Spike density. No. of florets per spikelet. Beak type. Ratio of glume width to length.	

It has previously been noted that the spring habit of growth of the wheat was highly dominant and that the naked seed character of wheat was partially dominant. Thus, with respect to most characters the F_1 resembled the grass parent. In the case of spike density and glume width the dominance of the grass type was more pronounced in the F_1 of tetraploid wheat than of hexaploid wheat derivation. The observations of Tzitzin (44), Armstrong (4), Armstrong et al. (5) and Johnson (19) are in general agreement with the above.

In the F_2 and F_3 of hexaploid wheats × *A. elongatum* both parental types of most characters were generally recovered. Whether inherited from the grass or the wheat the recovery of the recessive type was generally low. For most quantitative characters the modal classes of the F_2 and F_3

were of an intermediate type. Transgressive segregation was noted in beak type, awning and ratio of glume width to length. For several characteristics it was found that the F_4 were less variable than previous segregating generations.

In the case of characters in which the grass type was highly or partially dominant the 1st generation after backcrossing to wheat showed some but not a pronounced reduction in the dominance of the grass type. Due to the irregularities of meiotic behaviour resulting in the loss of chromatin material and due to gametic elimination, it was considered invalid to attempt to interpret the segregation of characters on a factorial basis.

Forage Quality

A. elongatum is rather undesirable as a forage grass. Early in the season the plants are very leafy and the leaves fairly soft. As the season advances the leaves become stiff and harsh. The stolid stems are quite coarse and very hard. All of these facts indicate that the plant would not be relished by stock, either as pasture or as hay. It was hoped that the hybrids involving *A. elongatum* would be more desirable in forage qualities through their endowment from the wheat parents.

In Table 15 it has been shown that the F_1 hybrids displayed a partial dominance of the grass type of stem and of leaf texture. It is thus obvious that the F_1 are of rather low forage quality.

The F_2 to F_4 were generally similar to the F_1 in leaf texture. In these segregating generations no plants were found with a desirable soft leaf. The occasional plant in the generations after backcrossing to the wheat parents was of a more desirable forage type.

With respect to leafiness, quite marked difference showed up in the F_4 generation. Certain F_3 plants gave rise to F_4 lines which were uniformly lacking in leafiness, while the progenies of other F_3 plants of the same cross were fairly uniformly leafy. There were also variations in the extent to which the leaves were basal or carried up the stem, and this condition was also fairly homozygous within lines in the F_4.

Disease Resistance

A. elongatum has been reported by Tzitzin (44) to be resistant to smut, mildew and rust, and Veruskin (55) noted that it was resistant to fungus diseases in general. A severe stem and leaf rust epidemic in 1938 afforded an opportunity to observe the rust resistance of the hybrid material.

Neither leaf nor stem rust has ever been observed on F_1, F_2, or F_3 plants, all of which were growing under rust conditions in 1938. The F_4 grown in 1939 was likewise free of infection, although the disease was not very prevalent in that year.

After backcrossing the F_1 to the rust susceptible wheat parents, some stem rust susceptible plants have appeared in the 1st to 3rd generation progenies. In 1938, after backcrossing to Little Club, 1 out of 12 plants was severely attacked by stem rust. In 1939 in the 2nd generation backcross involving Marquis 1 plant out of 12, and in the 3rd generation back-

cross involving Marquis 3 plants out of 77 were severely attacked by stem rust. No rust has been observed on comparatively large progenies of backcrosses to Apex and Hope.

The non-backcrossed populations have thus a high degree of resistance to rust, a fact also noted by Tzitzin (44), and in a general way by Lapin (26) and Veruskin (55). The fact that the F_1 to F_4 of rust susceptible varieties, such as Marquis, were rust resistant is evidence that the grass parent contributed factors for rust resistance. The resistance obtained from the grass is highly dominant and apparently dependent upon several factors as no susceptible plants appeared in fairly large populations, and even in backcrossed progenies the proportion of susceptible plants was small.

The only other disease observed in the hybrids was ergot caused by *Claviceps* sp. Although Johnson (19) states that "the characteristic ergot immunity of *A. elongatum* is reflected in its hybrids", this disease was prevalent in the F_1 hybrids of *A. elongatum* parentage at Saskatoon and Melfort. The prevalence of the disease decreased as fertility increased with advancing generations, and thus the incidence of the disease was related to the opportunity for infection. In highly sterile plants the flowering glumes remained open for a long period, exposing the flower to infection. In fertile plants the flowers were exposed for a much shorter time.

CHARACTERISTICS OF PROGENIES OF *A. GLAUCUM* PARENTAGE

Vigour and Growth Habits

A. glaucum is shorter and, in general, less growthy than *A. elongatum*. The F_1 of *A. glaucum* parentage were considerably taller growing, and stooled more profusely than the wheat parents, and were somewhat more vigorous than the grass parent.

Rhizomes are found on some plants of *A. glaucum*. A proportion of the F_1 hybrids from this grass also displayed a tendency to creep, a fact noted by Johnson (19). The degree of expression of this character varied considerably, but in some plants the rhizome development was extensive.

The perennial habit of the grass was dominant in the F_1 hybrids. There were no characteristics indicative of an annual habit. In the year of seeding the F_1 of spring wheats $\times$ *A. glaucum* displayed the spring form of growth inherited from the wheat, while crosses involving winter wheats showed the winter habit of growth. In these respects the hybrids of *A. glaucum* parentage were similar to those of *A. elongatum* derivation.

Hardiness

The data on winter survival for the three winters 1936–37, 1937–38, and 1938–39 are summarized in Table 16.

From Table 16 it is seen that the tetraploid wheats gave rise to more hardy hybrids than the hexaploid wheats. This was also shown to be the case in the hybrids of *A. elongatum* parentage. This difference in survival is assumed to arise from the fact that the percentage of wheat chromosomes in hybrids of tetraploid wheat parentage is lower than in

TABLE 16.—WINTER SURVIVAL OF F_1 HYBRIDS OF SPECIES AND VARIETIES OF *Triticum* × *A. glaucum*

Female parent	Total no. of plants	Average percentage survival for 3 winters
		%
Tetraploid wheat derivatives		
T. dicoccoides	4	100.00
T. dicoccum	38	78.95
T. durum—		
Mindum	50	48.00
Pelissier	40	57.50
T. turgidum	11	90.91
T. timopheevi	67	97.01
T. pyramidale	44	75.00
Total and average	254	74.41
Hexaploid wheat derivatives		
T. vulgare—		
Marquis	32	53.12
Chinese	7	42.86
Hope	7	42.86
Karkov	53	35.85
Total and average	99	42.42
Grand total and average	353	65.44

hybrids derived from hexaploid wheat crosses. There is evidence that the wheat species and variety influenced survival. The progenies of *T. durum* parentage were lower in winter hardiness than the progenies of other tetraploid wheats. Contrary to expectation, the Karkov variety did not contribute greater hardiness to its hybrids than did the spring wheats.

The average survival of the F_1 of tetraploid wheats with *A. elongatum* and with *A. glaucum* was found to be 88.4% and 74.4% respectively, while that for the F_1 of hexaploid wheats with *A. elongatum* and with *A. glaucum* was 71.3% and 42.4% respectively. The average for the F_1 of all crosses of *A. elongatum* parentage was 83.4%, as compared to 65.4% for those of *A. glaucum* lineage. Thus the indications are that hybrids of *A. glaucum* parentage are less hardy than those from *A. elongatum*. On a priori grounds it might be presumed that in the decaploid *A. elongatum* there is a greater replication of genes affecting survival than in the hexaploid *A. glaucum*, and that this relationship would be reflected in the hybrids. These results are in agreement with those of Armstrong et al. (5) and Tzitzin (44).

Fertility

The data on the fertility of the F_1 hybrids of *A. glaucum* parentage are summarized in Table 17. These data are an average for a 3-year period. As shown by this table, the F_1 hybrids were almost completely sterile. Of the 222 plants harvested over the 3-year period, only one seed was obtained

TABLE 17.—SEED SETTING OF F_1 HYBRIDS OF CROSSES OF SPECIES AND VARIETIES OF *Triticum* WITH *A. glaucum*

Female parent	Total no. of plants harvested	Average percentage of harvested plants which were fertile	Average percentage of florets setting seed	Maximum fertility observed
Tetraploid wheat derivatives				
		%	%	%
T. dicoccoides	4	0.0	0.0	—
T. dicoccum	27	7.4	0.02	0.47
T. durum—				
Mindum	26	0.0	0.0	—
Pelissier	29	3.5	0.01	0.21
T. turgidum	12	8.3	0.02	0.25
T. timopheevi	37	0.0	0.0	—
T. pyramidale	46	4.4	0.1	0.24
Total and average	181	3.31	0.007	—
Hexaploid wheat derivatives				
T. vulgare—				
Marquis	22	0.0	0.0	—
Chinese	5	0.0	0.0	—
Hope	6	0.0	0.0	—
Karkov	8	0.0	0.0	—
Total and average	41	0.0	0.0	—

from each of 6 plants, all of which were derivatives of tetraploid wheat varieties. The hybrids of hexaploid wheat parentage were completely sterile.

An examination of the pollen from F_1 plants of wheat × *A. glaucum* revealed the fact that a very low percentage of grains were completely filled with cytoplasm. Of 2,889 grains examined from 29 plants, only 1.5% were classed as good. This figure compared with that of 4.0% and 30.4% good pollen found in the F_1 plants of tetraploid wheats × *A. elongatum* and hexaploid wheats × *A. elongatum*, respectively, shows that sporogenesis is considerably more irregular in hybrids of *A. glaucum* lineage than in those involving *A. elongatum*. This fact undoubtedly is the basis of the differences in fertility between the hybrids derived from the two grasses. Johnson (19) found that the anthers of F_1 plants of *A. glaucum* parentage failed to dehisce, and also that there was a very low percentage of good pollen produced by these hybrids.

From the 6 seeds obtained from F_1 plants involving *A. glaucum* only one gave rise to a mature plant. This plant was moderately vigorous, and was found to have a fertility of 12.5%. This represents a very substantial increase in fertility for one generation, being considerably more than the average but less than the maximum observed in *A. elongatum* F_2 hybrids.

The complete or almost complete sterility of F_1 hybrids of *A. glaucum* parentage was noted by Johnson (19), Johnson et al. (20), Armstrong et al.

(5), and was implied by Veruskin (52, 53) and Tzitzin (44) through their statements to the effect that the F_1 hybrids were generally sterile, but that the bread wheats $\times$ *A. elongatum* yielded some fertile hybrids. Cicin (8, 9) reported finding self fertile F_1 plants in *A. glaucum* hybrids. Hiznjak (17) stated that the F_1 of *Triticum* sp. $\times$ *A. glaucum* were sterile but elsewhere (22) reports that certain F_1 plants of *Triticum* $\times$ *A. intermedium (A. glaucum)* were highly self fertile. Sipkov (42) considered that certain races of *A. glaucum* were more closely related to *T. durum* than others, and consequently some F_1 plants were fertile and others sterile.

Seed Characters

The seed of *A. glaucum* with flowering glumes attached has an average 1000 kernel weight of approximately 4.5 grams. This is about one-sixth of the weight of the seed of bread wheats, and about two-thirds the weight of seed of *A. elongatum*. The general appearance of the seed of the two grass species is very similar, but in the seed of *A. glaucum* the caryopsis is readily removed from the seed coats, whereas it is removed with difficulty from seed of *A. elongatum*.

The F_0 seed derived from crosses of wheat $\times$ *A. glaucum* was very variable in weight. As an average, however, the F_0 seed derived from crosses involving tetraploid wheats was fairly plump, while the F_0 seed from hexaploid wheat crosses was rather poorly developed. Expressed as a percentage of the weight of normal seed of the wheat parents, the F_0 seed derived from hexaploid wheats on the average weighed 25.4%, as compared to an average of 51.6% for the F_0 seed derived from tetraploid wheats. Armstrong (4) and Armstrong et al. (5) report very similar results. Tzitzin (44) likewise noted that the F_0 seed from *T. vulgare* $\times$ *A. glaucum* had a low seed weight.

The F_0 seed from crosses of tetraploid wheats $\times$ *A. glaucum* averaged somewhat lower in weight than the F_0 seed from the same wheats crossed with *A. elongatum*. Contrary to this, Armstrong (4) and Armstrong et al. (5) report that the tetraploid wheats "gave slightly plumper seeds when crossed with *A. glaucum* than when crossed with *A. elongatum*". The writer found that on the average the F_0 seeds from crosses involving the hexaploid wheats was 2.5 times heavier from *A. elongatum* crosses than from *A. glaucum* crosses. This observation is in close agreement with that made by Armstrong (4) and Armstrong et al. (5).

In spite of the low seed weight, the F_0 seed of hexaploid wheats $\times$ *A. glaucum* had an average germination of 77.7%. This is not materially lower than the germination of the F_0 seed of tetraploid wheats $\times$ *A. glaucum* which was found to be 83.3%. This is evidence that there was practically no difference in embryo development between the F_0 seed derived from the two different groups of wheat. The marked differences in seed weight noted above must have been due to differences in endosperm development.

As already stated, only one F_2 plant of *A. glaucum* parentage was matured in 1939. The seed from this plant weighed 7.8 grams per 1000 kernels. This weight is somewhat higher than the 1939 average for that of the F_2 of the hexaploid wheats $\times$ *A. elongatum*.

Head Characters

A study of the characteristics of the F_1 hybrids as compared to the parents revealed that the grass type was partially dominant in the case of spike density and glume width, and highly dominant in the case of awning. The dominance of the grass type of spike density was less pronounced in the hexaploid wheat derivatives than in those of tetraploid wheat parentage. The dominance of the glume width of *A. glaucum* was less pronounced than the dominance of this character inherited from *A. elongatum*. This latter fact is probably due to the higher degree of polyploidy in *A. elongatum*, and thus a greater replication of genes affecting the character.

Forage Quality

The F_1 hybrids of *A. glaucum* parentage are reasonably desirable from the forage standpoint. In general, they are preferable to the *A. elongatum* derivatives in that they are more leafy, have the leaves carried up the stems to a greater height, and the foliage and culms are less coarse and harsh. Johnson (19) has also expressed a similar viewpoint. However, the hybrids involving *A. glaucum* are not completely desirable in that they inherit the solid stem of the grass, and the stem and leaves become fairly harsh early in the season.

Some differences in forage quality were apparent between the F_1 from different wheat species. The *T. pyramidale* × *A. glaucum* F_1 hybrids were the most desirable of all materials in the nurseries. The plants of this hybrid combination had more sterile culms resulting in greater leafiness, and had broader, softer leaves than those from any other cross. Johnson (19) reported that *Mindum* × *A. glaucum* F_1 hybrids had softer foliage than any other material which he had available. Khiznjak (23, 24) drew attention to the potentialities of the amphidiploids of *A. intermedium* (*A. glaucum*) parentage for fodder purposes.

Disease Resistance

The resistance of *A. glaucum* to smut, rust, and mildew was reported by Tzitzin (44) to be lower than that of *A. elongatum*. Johnson (19) stated that *A. glaucum* was fairly susceptible to ergot. Both of these investigators reported that the lower degree of resistance of *A. glaucum* to these diseases was reflected in the hybrids involving this species. At Saskatoon *A. glaucum* was never observed to be attacked by stem rust, leaf rust, smut or ergot, and the F_1 of crosses involving this species were free from attack by the rusts and by smut. The F_1 were, however, very heavily attacked by ergot. The prevalence of this disease among the F_1 is considered to be largely the result of the almost complete sterility of this material. Because of the failure of fertilization the florets remain open and provide an opportunity for infection over a long period. There was, however, some indication of more susceptibility to this disease in the case of hybrids of *A. glaucum* parentage than of those of *A. elongatum* derivation. Johnson (19) reached a similar conclusion.

DISCUSSION

In interspecific crosses of hexaploid wheat with tetraploid wheat Thompson (48) has reported that "a large proportion of the F_2 and an increasing proportion in later generations possess a combination of characters found in one or other of the parental types". "In general the proportion with various recombination of characters is far below Mendelian expectation". Thompson found that the cytological basis for such a genetic result is that "most F_2 plants have one or the other of the parental chromosome numbers or some number approaching these". On the other hand, in the F_2 of crosses of hexaploid wheats with tetraploid wheats Harrington (16a) and others have found that intermediate character expressions are of fairly frequent occurrence, and that a considerable proportion of the F_2 displayed a recombination of parental characters. It was considered of interest to examine the segregating generations of *Triticum-Agropyron* with respect to the recombination of characters.

The barriers of sterility limited the study of character recombinations to the progenies of hexaploid wheats $\times$ *A. elongatum*. It was also essential to confine the study to quantitative characters by which the parents were readily distinguished. For this purpose spike density, glume width, and ratio of glume width to length were selected. The range of the parental types was determined for each character, and in each F_2 and F_3 plant the expression of each of the three characters was designated as wheat-like, intermediate or grass-like. Thus, a plant might be classified as grass-like for spike density and intermediate for the other two characters, while another plant might be wheat-like for spike density, grass-like for glume width, and intermediate for the ratio. In all, 279 F_2 plants and 419 F_3 plants were classified in this manner. Figure 2 illustrates the character combinations in the F_2 population.

With three characters, each with 3 degrees of expression, there existed a possibility of 27 different combinations. As shown by the figure, only 12 of these were actually obtained. This recovery of less than one-half of the total possible combinations was, however, probably not highly significant in such a relatively small population. It is clearly evident from the figure that there was not a large proportion of the plants having the combination of characters of the parents. No plants wheat-like for all characters were obtained, and only slightly more than one-quarter of the plants were grass-like for all characters. A recombination of characters was found in 202, or 72%, of the 279 plants.

The condition found in the F_3 population of 419 plants was essentially similar to that given above for the F_2; 15 of the possible 27 character combinations were recovered. As in the F_2, no plants having a wheat-like combination of characters were found, and only 9% of the plants were grass-like for all characters. Conversely, over 90% of the F_3 plants showed a recombination of characters.

Underlying and related to this evidence of character recombinations is the cytological finding of Peto (35) and others that the F_2 have a chromosome number approximately intermediate between the parental chromosome number, and showing no tendency to revert to one or the other parental number, as in the case of crosses of common with emmer wheats.

Having established that a considerable proportion of the F_2 and F_3 exhibited character recombinations, the question arose as to whether or not the recombinations occurred at random. In order to secure information

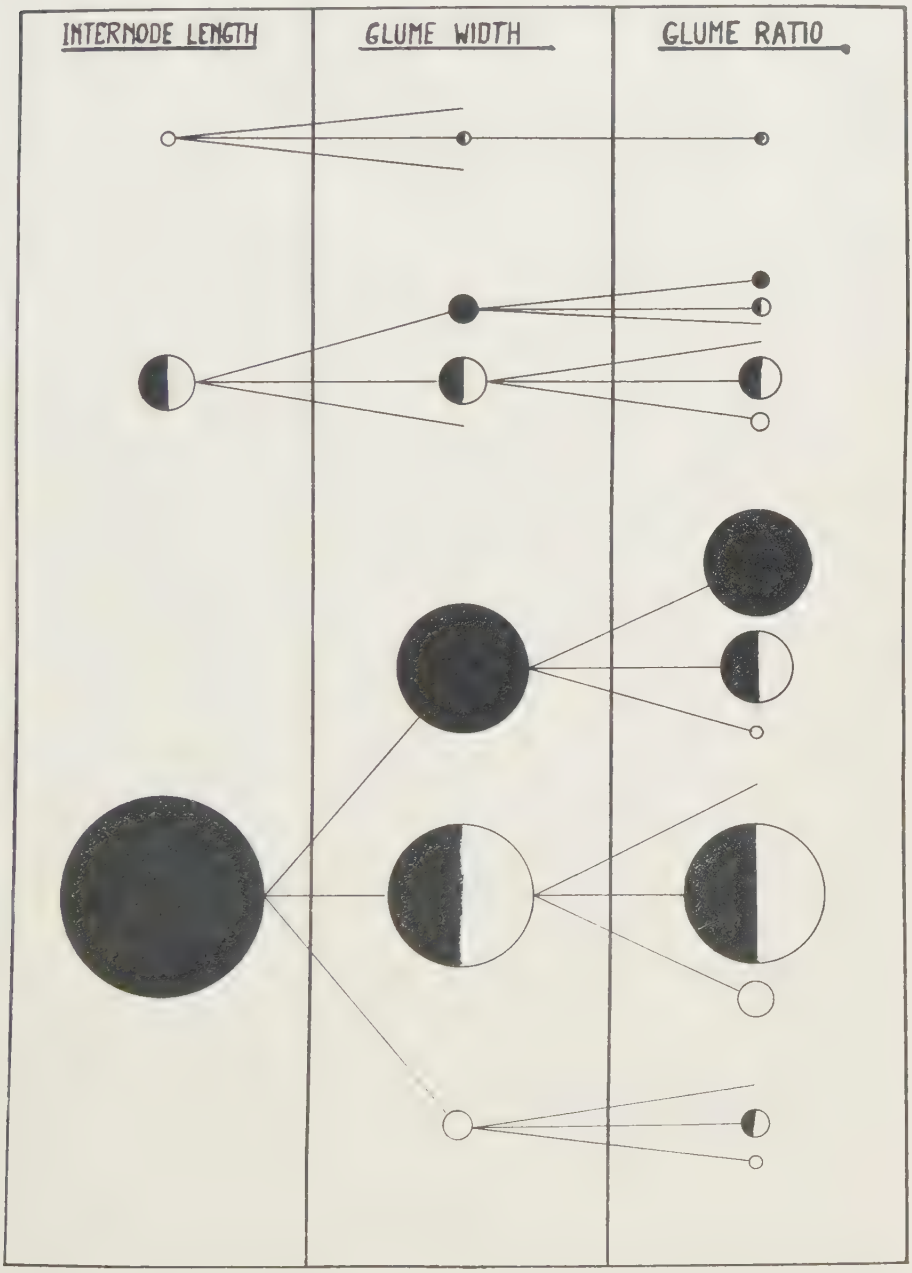

FIGURE 2. Various combinations of three characters found in an F_2 population of 279 plants of *T. vulgare* × *A. elongatum*. Clear circles—wheat-like expression, half black circles—intermediate expression, and solid black circles—grass-like expression. Area of circles in proportion to number of plants displaying character.

in this connection, the X^2 test for the independence was used to determine the association of spike density with glume width, and of spike density with ratio of glume width to glume length in 279 F_2 plants and 419 F_3 plants.

Table 18 gives a summary of the X^2 for independence data for all the associations studied.

TABLE 18.—SUMMARY OF DATA ON X^2 FOR INDEPENDENCE OF SPIKE DENSITY WITH GLUME WIDTH AND OF SPIKE DENSITY WITH RATIO OF GLUME WIDTH TO GLUME LENGTH

Generation	Spike density with glume width			Spike density with ratio of glume width to length		
	X^2	n	P	X^2	n	P
F_2	2.2245	1	Between 0.20 and 0.10	3.1786	1	Between 0.10 and 0.05
F_3	2.7221	1	Between 0.10 and 0.05	3.8995	1	Between 0.05 and 0.01

The probability of association was found to be less than $P = 0.05$ in the case of spike density with ratio of glume width to glume length. Thus, there was an indication that the segregation of these 2 characters was associated and not random. For the other 3 associations studied, the P values were all above the level of significance, and thus it was impossible to demonstrate that the associations were not random. However, in these cases the fact that the P values were all low and approached the accepted level of significance suggested that the recombinations were not completely random.

In the cross between *Nicotiania alata* and *N. Langsdorffi* Anderson (2) demonstrated that the recombinations in the F_2 were less than one-sixty-fourth of the imaginable recombinations and brought forward evidence to show that gametic elimination, zygotic elimination, pleiotropism, and linkage all operated to hinder recombination. In the *Triticum-Agropyron* hybrids there was evidence of gametic and zygotic elimination, and on a priori grounds it may be assumed that the other two factors are also operating to reduce the amount of recombination. The fact that the *Triticum* species differs from *Agropyron elongatum* in chromosome number suggests that in hybrids of this intergeneric cross the gametic and zygotic elimination would be greater, and consequently the amount of imaginable recombination lower than in the cross of *M. alata* × *N. Langsdorffi* in which no differences in chromosome number are involved.

SUMMARY

1. This paper presents the results to date of a breeding program involving crossing *Triticum* sp. with *Agropyron* sp. with the object of developing a large seeded perennial forage grass.

2. The parental material consisted of *Haynaldia villosa*, 12 species of *Triticum*, and 10 species of *Agropyron*. In crossing the wheats were generally used as the female parent.

3. The species and varieties of *Triticum* failed to hybridize with the following species of *Agropyron: A. repens*, *A. subsecundum*, *A. smithii*, *A. pauciflorum*, *A. cristatum*, *A. inerme*, and *A. junceum*. A low degree of success was obtained in crosses with *A. trichophorum*.

4. All species of wheat, excepting *T. monococcum*, were successfully crossed with *A. elongatum*. Crosses were also successfully made between *A. glaucum* and all species of wheat, excepting *T. sphaerococcum*. The crossing success with tetraploid wheats was about twice as high as with hexaploid wheats. *A. elongatum* was considerably more compatible than *A. glaucum* in crosses with the wheats.

5. The F_1 plants of tetraploid wheats $\times$ *A. elongatum* and the F_1 of all crosses involving *A. glaucum* were highly sterile when backcrossed, using the wheat as the male parent. The F_1 plants of hexaploid wheats $\times$ *A. elongatum* were partially fertile when backcrossed to wheat, but of lower fertility when backcrossed to the grass parent.

6. Assuming that "ripening off" indicated annual habit, the F_1 of wheat $\times$ *A. elongatum* were all perennial, while the segregating generations consisted of a small proportion of annuals. Backcrossing to wheat increased the proportion of annual forms.

7. The F_1 of wheat $\times$ *A. elongatum* had a high winter survival. The survival of the F_1 derived from tetraploid wheats was higher than that of the F_1 of hexaploid wheat parentage. The F_1 derived from winter wheat varieties did not survive better than the F_1 derived from spring wheat varieties. Survival decreased by at least 50% with each advance in generation. Backcrossing to wheat resulted in a material drop in survival, but backcrossing to *A. elongatum* resulted in greater hardiness. Marked differences between the hardiness of different F_3 lines demonstrated that survival was largely determined by genetic factors.

8. The fertility of the F_1 of *A. elongatum* parentage was dependent upon the chromosome group of the wheat parent. The F_1 derived from diploid wheat *(H. villosa)* were completely sterile, the F_1 derived from tetraploid wheats were very highly sterile, while the F_1 derived from hexaploid wheats were partially fertile. Fertility displayed a definite trend to increase with each advance in generation. Backcrossing the F_1 to wheat resulted in a substantial increase in fertility, as compared to non-backcrossed material. The 2nd and 3rd backcross generations derived from Hope, and the 2nd backcross generation derived from Little Club parentage had exceptionally high fertility.

9. F_0 seed was fairly plump, and there was no difference in the relative plumpness of F_0 seed of tetraploid wheats $\times$ *A. elongatum*, and F_0 seed of hexaploid wheats $\times$ *A. elongatum*. There was a definite trend for the seed weight of hexaploid wheat derivatives to decline with each advance in generation. In the backcross progenies no such trend was evident, and the occasional plant produced exceptionally heavy seed.

10. In the F_1 plants of *A. elongatum* parentage the grass type of the following characters was found to be partially dominant: primary root number, primary leaf vein number, stem hollowness, leaf texture, head density, number of florets per spikelet, beak type, and ratio of glume width to length. The grass characteristics were highly dominant in the case of

perennial habit, awning, and glume width. The naked seed of wheat was partially dominant to the grass character. The spring habit of growth of the spring wheats was dominant to the winter habit of the grass. Thus, with respect to most characters the F_1 were more grass-like than wheat-like.

11. In the case of spike density and glume width the dominance of the grass character was more pronounced in the F_1 of tetraploid wheats $\times$ *A. elongatum* than in the F_1 of hexaploid wheats $\times$ *A. elongatum*.

12. In the F_2 and F_3 of hexaploid wheats $\times$ *A. elongatum* both parental types of most characters were recovered. Whether the recessive type was inherited from the grass or the wheat, the recovery of the recessive type was usually low. For most quantitative characters the modal classes of the F_2 and F_3 were of an intermediate type. Transgressive segregation was noted in the case of beak type, awning, and ratio of glume width to length. For several characters the F_4 was less variable than previous segregating generations.

13. In general, the forage quality of the hybrids of *A. elongatum* parentage was low.

14. Stem rust appeared only on hybrid material of *A. elongatum* parentage in the case of backcrosses to rust susceptible wheat varieties. Ergot was the only other disease observed, and the incidence of this disease was related to the sterility of the hybrids.

15. The F_1 of wheat $\times$ *A. glaucum* displayed hybrid vigour, and were perennial. A tendency to produce rhizomes was inherited from the grass parent. The spring habit of growth inherited from the spring wheats was dominant.

16. The F_1 of hexaploid wheats $\times$ *A. glaucum* were less winter hardy than the F_1 of tetraploid wheats $\times$ *A. glaucum*. There was an indication that the F_1 of *A. glaucum* parentage were less hardy than the F_1 of *A. elongatum* parentage.

17. Almost complete sterility characterized the F_1 hybrids of *A. glaucum* parentage. The pollen development was very poor in these hybrids.

18. The F_0 seed of tetraploid wheats $\times$ *A. glaucum* was fairly plump, but the seed of hexaploid wheat $\times$ *A. glaucum* was poorly developed. The germination of F_0 seed was surprisingly high.

19. In F_1 hybrids of *A. glaucum* parentage the grass type was partially dominant in the case of spike density, glume width, and rhizome development, and was highly dominant in the case of awning and perennial habit. The spring habit of growth was the only wheat character which was dominant. The derivatives of hexaploid wheats were less grass-like with respect to spike density than the F_1 of tetraploid wheat parentage. The dominance of the glume width of *A. glaucum* was less pronounced than the dominance of this characteristic of *A. elongatum*.

20. In general, the F_1 hybrids of *A. glaucum* were fairly desirable from a forage standpoint. They excelled the F_1 of *A. elongatum* derivation in this regard.

21. Ergot was the only disease observed to be prevalent among F_1 hybrids of *A. glaucum* parentage.

22. In the F_2 and F_3 of *T. vulgare* × *A. elongatum* it was shown that a large proportion of the plants displayed a recombination of parental types. In the F_3 it was found that the segregation of spike density was not independent of the segregation of ratio of glume width to glume length. It was impossible to demonstrate that three other associations studied were not independent, but the low P values indicated that the recombinations were not completely at random.

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REFERENCES

1. Aase, Hannah C. Cytology of cereals. Botanical Review I : 467-496. 1935.
2. Anderson, E. Recombination in species crosses. Genetics 24 : 668-698. 1939.
3. Anonymous. Perennial wheat in U.S.S.R. Jour. Amer. Soc. Agr. 28 : 1061-1062. 1936.
4. Armstrong, J. M. Hybridization of *Triticum* and *Agropyron*. I. Crossing results and description of first generation hybrids. Can. J. Research, C, 14 : 190-202. 1936.
5. Armstrong, J. M., W. J. White, H. A. McLennan, and L. P. V. Johnson. Genetic investigations in *Triticum Agropyron* hybrids. Paper read at the Seventh International Genetics Congress, Edinborough. 1939.
6. Berg, K. H. Cytologische Untersuchungen an *Triticum turgidovillosum* und seinen Eltern. Zeits. Induk. Abst. Vererb. 67 : 342-373. 1934.
7. Blakeslee, A. F. and A. G. Avery. Methods of inducing chromosome doubling in plants by treatment with colchicine. Science. 86 : 408. 1937.
8. Cicin, N. V. Problems of winter and perennial wheat. Seljozgex, Moscow. 1935 p. 101. (Herb. Abstr. 7 : 203-204. 1937.) Original not seen.
9. Cicin, N. V. The problem of perennial wheat. Selek. semenovod. No. 2: 21-27. 1936. (Herb. Abstr. 7 : 14-15. 1937). Original not seen.
10. Dorsey, E. Chromosome doubling in the cereals. J. Hered. 30 : 393-395. 1939.

11. East, E. M. Genetic reactions in *Nicotiana*. I. Compatibility. Genetics, 20 : 403-413. 1935.

12. Florell, O. H. Bulked population method of handling cereal hybrids. Jour. Amer. Soc. Agron. 21 : 718-724. 1929.

13. Gaiser, L. O. Chromosome numbers in Angiosperms. Genetica. 12 : 161-320. 1930.

14. Hayes, H. K., and O. S. Aamodt. Inheritance of winter hardiness and growth habit in crosses of Marquis with Minhardi and Minturki wheats. Jour. Agr. Research, 35 : 223-236. 1927.

15. Hayes, H. K. and R. J. Garber. Breeding crop plants. McGraw-Hill Book Co., New York. 2nd Ed. 1927.

16. Hitchcock, A. S. Manual of the grasses of the United States. U.S.D.A. Misc. Pub. 200. 1935.

16a. Harrington, J. B. Character combinations in relation to endosperm development in inter-specific *Triticum* crosses. Can. J. Research, C, 13 : 388-399. 1935.

17. Hiznjak, V. A. A cyto-genetical study of *Triticum* × *Agropyron* hybrids and the trend in breeding perennial wheat. Preliminary contribution. Trudy Azovo-Cernomor. Selekcent. No. 1 : 25-30. 1936. (Herb. Abstr. 7 : 206-207. 1937.) Original not seen.

18. Johnson, L. P. V. and H. A. McLennan. Hybridization of *Triticum* and *Agropyron*. III. Crossing technique. Can. J. Research, C, 15 : 511-519. 1937.

19. Johnson, L. P. V. Hybridization of *Triticum* and *Agropyron*. IV. Further crossing results and studies on the F_1 hybrids. Can. J. Research, C, 16 : 417-444. 1938.

20. Johnson, L. P. V., H. A. McLennan, and J. M. Armstrong. Fertility and morphological characters in *Triticum-Agropyron* hybrids. Genetics, 24 : 91-92. 1939.

21. Krasnjuk, A. A. *Secale cereale* × *Agropyron cristatum* hybrids. Social Zern. Hoz. No. 1 : 106-115. 1935. (Herb. Abstr. 6 : 81. 1936.) Original not seen.

22. Khiznjak, V. A. Form development in *Triticum-Agropyron* hybrids and the production of perennial wheats. Breeding and Seed Growing (Russian). No. 12 : 20-33. 1936. (Pl. Breed. Abstr. 7 : 384-385. 1937.) Original not seen.

23. Khiznjak, V. A. Wheat-quitch amphidiploids. C.R. (Doklady) Acad. Sci. U.R.S.S. 17 : 489-90. 1937. (Pl. Breed. Abstr. 8 : 240. 1938.) Original not seen.

24. Khiznjak, V. A. Wheat-*Agropyron*—a new useful fodder crop plant. Breeding and Seed Growing (Russian). No. 11 : 56-57. 1937. (Pl. Breed. Abstr. 8 : 459. 1938.) Original not seen.

25. Khijnyak, V. A. Form genesis in wheat-*Agropyron* hybrids. Bull. Acad. Sci. U.R.S.S., Ser. Biol. 597-626. 1938. (Pl. Breed. Abstr. 9 : 295-296. 1939.) Original not seen.

26. Lapin, M. M. On the research of N.V. Cicin with *Triticum Agropyron* hybrids. Bull. Vsesojuz Akad. Nauk. No. 7 : 29-30. 1935. (Herb. Abstr. 6 : 441. 1936.) Original not seen.

27. Muntzing, A. Hybrid incompatibility and the origin of polyploidy. Hereditas. 18 : 33-55. 1933.

28. Oehler, E. Untersuchungen en *Aegilops-Haynaldia*-und *Triticum Haynaldia*-Bastarden. Zeits. Induk. Abst. Vererb. 68 : 187-208. 1935.

29. Percival, J. The wheat plant—A monograph. Duckworth, London. 1921.

30. Peto, F. H. Cytological studies in the genus *Agropyron*. Can. J. Research, 3 : 428-448. 1930.

31. Peto, F. H. Hybridization of *Triticum* and *Agropyron*. II. Cytology of the male parents and F_1 generation. Can. J. Research, C, 14 : 203-214. 1936.

32. Peto, F. H. *Triticum-Agropyron* hybridization studies. Unpublished report. 1938.

33. Peto, F. H. Hybridization of *Triticum* and *Agropyron*. V. Doubling the chromosome number in *T. vulgare* and F_1 of *T. vulgare* × *A. glaucum* by temperature treatments. Can. J. Research, C, 16 : 516-529. 1938.

34. Peto, F. H. Chromosome doubling induced by temperature shocks in hybrid zygotes of *Triticum vulgare* pollinated with *Agropyron glaucum*. Genetics. 24 : 93. 1939.

35. PETO, F. H. Fertility and meiotic behavior in F_1 and F_2 generations of *Triticum-Agropyron* hybrids. Genetics. 24 : 93. 1939.

36. PETO, F. H. and J. W. BOYES. Hybridization of *Triticum* and *Agropyron*. VI. Induced fertility in Vernal emmer × *A. glaucum*. Can. J. Research, C, 18 : 230-239. 1940.

37. POWERS, LEROY. The nature of interaction of genes differentiating habit of growth in a cross between varieties of *Triticum vulgare*. Jour. Agr. Research, 49 : 573-605. 1934.

38. RANDOLPH, L. F. Some effects of high temperature on polyploidy and other variations in maize. Proc. Nat. Acad. Sci. 18 : 222-229. 1932.

39. SAPEHIN, A. A. Cytological investigation of *Triticum* × *Agropyron* hybrids. J. Bot. U.R.S.S. 20 : 119-125. 1935. (Pl. Breed. Abstr. 6 : 43. 1935.) Original not seen.

40. SHIBAEY, P. N. Grain quality of couch grass and wheat-couch grass hybrids. Cereal Chemistry, 14 : 437-439. 1937.

41. SIMONET, M. Contribution a l'etude cytologique et genetique de quelques *Agropyrum*. C. R. Acad. Sci. Paris. 201, 1210-2. 1935. (Herb. Abstr. 6 : 275. 1936.) Original not seen.

42. SIPKOV, T. P. A contribution to the cytology of *Triticum-Agropyron* hybrids. Bull. Appl. Bot. Leningrad. Ser. 11 (9) : 357-360. 1935. (Pl. Breed. Abstr. 7 : 45. 1936.) Original not seen.

43. SULLIVAN, J. T. and W. M. MYERS. Chemical composition of diploid and tetraploid *Lolium perenne*. L. Jour. Amer. Soc. Agron. 31 : 869-871. 1939.

44. TZITZIN, N. V. The *Triticum* × *Agropyron* hybrids. Lenin Acad. Agric. Sci. Siberian Inst. Grain Cult. Omsk. 101. 1933. (Abridged translation.)

45. TZITZIN, N. V. Breeding *Triticum-Agropyron* hybrids. Bull. Lenin Acad. of Agric. Science. No. 10 : 1-4. 1936. (Pl. Breed. Abstr. 7 : 385. 1937). Original not seen.

46. TZITZIN, N. V. The problem of *Triticum-Agropyron* hybrids. Ogiz.-Selkhozgiz. 1937. p. 235. (Pl. Breed. Abstr. 9 : 47-50. 1939.) Original not seen.

47. THOMPSON, W. P. Causes of difference in success of reciprocal interspecific crosses. Amer. Nat. 64 : 407-421. 1930.

48. THOMPSON, W. P. The causes of the cytological results obtained in species crosses in wheat. Can. J. Research, 10 : 190-198. 1934.

49. THOMPSON, W. P. The causes of hybrid sterility and incompatibility. Paper read at meeting of Genetics Society of America, Ottawa, Canada. 1938.

50. THOMPSON, W. P. The frequency of fertilization and the nature of embryo and endosperm development in intergeneric crosses in cereals. Paper read at the Seventh International Genetics Congress, Edinborough. 1939.

51. VERUSHKINE, S. and A. SHECHURDINE. Hybrids between wheat and couch grass. J. Hered. 24 : 329-335. 1933.

52. VERUSHKINE, S. M. On the way towards perennial wheat: *Triticum* × *Agropyron* hybrids. Social Zern Hoz. No. 4 : 77-83. 1935. (Herb. Abstr. 6 : 82. 1936.) Original not seen.

53. VERUSHKIN, S. M. The main trend in the work with *Triticum* × *Agropyron* hybrids at the Saratov station. Selek. Semenovod. No. 8 : 23-25. 1936 (Herb. Abstr. 7 : 15. 1937.) Original not seen.

54. VERUSKIN, S. M. Hybridization of *Triticum* with *Agropyron*. Ogiz. Saratov, 1935. p. 39. (Herb. Abstr. 7 : 205. 1937.) Original not seen.

55. VERUSKIN, S. The main trend in work with *Triticum* × *Agropyron* hybrids at the Saratov plant breeding station. Pod Znam. Marx. No. 7 : 144-158. 1936. (Herb. Abstr. 7 : 206. 1937.) Original not seen.

56. WAKAR, B. A., E. B. KROT, and L. A. BREKMA. Studies on wheat hybrids. Cytological memoir. Lenin. Acad. Agric. Sci., Siberian Inst. Grain Cult., Omsk. 1934. p. 106. (Pl. Breed. Abstr. 5 : 313-315. 1935.) Original not seen.

57. WAKAR, B. A. Cytologische Untersuchung der ersten Generation der Weisen-Queckengras Bastarde. Der Zuchter, 7 : 199-206. 1935.

58. WAKAR, B. A. A cytological analysis of wheat × couch grass hybrids. Siberian Grain Res. Inst. Omsk. 1935. p. 31. (Pl. Breed. Abstr. 7 : 43-44. 1936.) Original not seen.

59. WAKAR, B. A. Cytology of *Triticum-Agropyron* hybrids. Ogiz, Omsk. 1935. p. 64. (Herb. Abstr. 7 : 204. 1937.) Original not seen.

60. WAKAR, B. A. Wheat-*Agropyron* hybrids : a hylogenetic investigation. Trudy. prikl. Bot. Genet. i. Selekcii. Ser II. No. 8 : 121-161. 1935. (Herb. Abstr. 6 : 274-275. 1936.) Original not seen.

61. WAKAR, B. A. Cytologische Untersuchung uber F_1 der Weizen-Queckengras Bastarde. Cytologia, 7 : 293-312. 1936.

62. WAKAR, B. A. Cytologische Untersuchung der $F_1 - F_6$ Bastard von *Triticum vulgare* (Host.) × *Agropyron intermedium* (Host.) P.B. Bull. Acad. Sci. U.R.S.S. Series Biol. Hr. 3 : 621-640. 1938. (Pl. Breed. Abstr. 9 : 296. 1939.) Original not seen.

63. WATKINS, A. E. The wheat species—A critique. Jour. Genet. 23 : 173-263. 1930.

64. WATKINS, A. E. Hybrid sterility and incompatibility. Jour. Genet. 25 : 125-162. 1932.